PHYSICAL MECHANISMS FOR VARIATION IN PINK SALMON (*ONCORHYNCHUS GORBUSCHA*) SURVIVAL WITHIN THE UPWELLING AND DOWNWELLING DOMAINS OF THE NORTHEAST PACIFIC

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By

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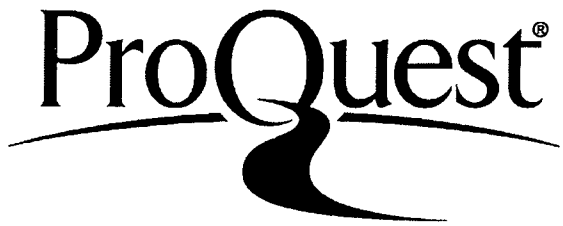

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PHYSICAL MECHANISMS FOR VARIATION IN PINK SALMON (*ONCORHYNCHUS GORBUSCHA*) SURVIVAL WITHIN THE UPWELLING AND DOWNWELLING DOMAINS OF THE NORTHEAST PACIFIC

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ABSTRACT

Regional coastal conditions have a strong influence on juvenile salmon (genus *Oncorhynchus)* survival during their critical first months in the marine environment. Salmon survival has been thought to be favored within the downwelling domain if water column stabilities increase, whereas stability may have the opposite effect at lower latitudes. To explore this hypothesis at a local scale, we examined the relationship between stability and the characteristics of growth rate, condition, and marine survival of several stocks of pink salmon (*O. gorbuscha*) within Prince William Sound (PWS) and two water masses, Alaska Coastal Current and shelf, in the northern coastal Gulf of Alaska (GOA). While slower and weaker development of stratification with a deeper mixed layer depth may be more important for juvenile pink salmon survival in the Sound, earlier and stronger stratification with a shallower mixed layer depth may be more beneficial within the Gulf. As expected, stability within PWS did explain the growth rate of hatchery fish, although stability explained only a small amount of the variability and did not have the same relationship for each hatchery stock. Contrary to expectation, stability just prior to capture did not explain the variability in condition index for either hatchery or wild fish collected from within the Sound or from within either GOA water mass. When stability was below average just prior to capture within PWS, the relationship between condition index and year-class survival was positive; when stability was above-average just prior to capture, the relationship was negative. In a broader scale study, we explored the relationships between regional water column stabilities during early marine residence of pink salmon in both upwelling and downwelling domains of the northeast Pacific Ocean and marine survival rates the following year for hatchery stocks ranging from Vancouver Island, British Columbia, to Kodiak Island, Alaska. Contrary to expectation, our findings were similar between the upwelling and downwelling areas, but differed by the distance offshore. Marine survival rates of hatchery pink salmon from northern and southern stocks increased for salmon that experienced below-average stability on the inner shelf during early marine residence while stability effects from the outer shelf showed no consistent relationship to marine survival.

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GENERAL INTRODUCTION

During early marine residence, warm anomalies in coastal sea surface temperatures (SSTs) are associated with an increase in survival rate for Alaskan sockeye (*Oncorhynchus nerka*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon stocks and a decrease in survival rate for sockeye and pink salmon stocks from British Columbia and Washington (Mueter *et al.,* 2002a). Besides the environmental covariate SST, other studies have focused on stability-induced changes in the availability of light and nutrients for the production of phytoplankton that are reflected in secondary production that could then ultimately affect the marine survival rates of juvenile salmon (Gargett, 1997). Regional coastal conditions have a greater influence on salmonid survival rates and recruitment than large-scale climate patterns (Pyper *et al.,* 2001; Mueter *et al.,* 2002a; Mueter *et al.*, 2002b). Survival rates in the upwelling (Baja California to Vancouver Island) and downwelling domains (Queen Charlotte Sound to the Aleutian Islands) of the northeast Pacific Ocean are often asynchronous (Francis and Sibley, 1991). Salmon survival should be favored within the downwelling domain if water column stabilities increase, whereas stability should have the opposite affect at lower latitudes (Gargett, 1997). Cooler SSTs during the winter prior to smolt migration, which are associated with weaker spring stratification, lead to higher smolt to adult survival of Oregon Production Index coho salmon (*O. kisutch*) in the upwelling domain (Logerwell *et al.,* 2003). In the downwelling coastal Gulf of Alaska (GOA), increased SST strengthens water column stability, which is linked to increased chlorophyll-*a* concentrations, longer bloom duration, and earlier onset of the spring bloom (Henson, 2007).

This study explored the relationship between water column stabilities during early marine residence and marine survival rates of pink salmon stocks at both a local (Chapter 1 and 2) and broad (Chapter 3) scale within the northeast Pacific Ocean. Using a comprehensive pink salmon database that included almost 25,000 individuals (10,000 of which were hatchery otolith marked) collected from Yakutat to Kodiak Island, Alaska, by four organizations (Alaska Department of Fish and Game, NOAA National Marine

Fisheries Service Auke Bay Laboratory Ocean Carrying Capacity Program, University of Alaska Fairbanks (UAF) GLOBEC, and the UAF APEX project), along with synchronous oceanographic data collected nearby, there existed a unique opportunity to test the optimal stability 'window' hypothesis on a fine scale. Chapters 1 and 2 examined how oceanographic conditions within Prince William Sound (PWS) and the northern coastal GOA affected the growth, condition, and ultimately the survival of hatchery and wild pink salmon stocks originating from within the Sound.

Measures of growth rate and body condition can be used as indicators of habitat quality and to identify links between regional oceanographic conditions and juvenile salmon survival, which is thought to depend on growth (Mueter *et al.,* 2002a; Brodeur *et al.,* 2004). In Chapter 2, it was postulated that growth rate and fish condition should increase with decreasing stability within PWS because slower and weaker development of stratification with a deeper mixed layer depth may enhance juvenile pink salmon survival in the Sound (Eslinger *et al.,* 2001). During cooler, stormier springs, phytoplankton blooms are prolonged and do not intensify as quickly due to the presence of a deeper mixed layer. Through periodic interruptions from increased winds remixing the water column and resupplying nutrients to the surface, phytoplankton production is lengthened, the interaction between phytoplankton and the springtime zooplankton community is prolonged, and more organic matter is retained in pelagic food webs (Eslinger *et al.,* 2001).

The oceanographic processes that affect early marine mortality are believed to be quite different in the Gulf (Cooney, 1993). Within the Gulf, it was postulated that fish condition should increase with increasing stability. During the winter and early spring, vertical mixing is not suppressed and macronutrients are plentiful since water column stability is low and the mixed layer depth is deep. Primary production is light limited, though, resulting in low overall production in the system. During the spring, solar radiation strengthens and warms the surface layers so that mixing is inhibited by the increase in the water column stability and shallowing of the mixed layer depth (Miller,

2004). With sufficient light levels, an increase in primary production during the spring bloom should lead to elevated secondary production and higher survival rates of salmon in the GOA. For the third hypothesis in Chapter 2, it was postulated that fish condition and environmental factors, such as water column stability, should predict year-class survival for juvenile pink salmon.

While Chapters 1 and 2 examined the relationship between regional water column stability and the characteristics of growth rate, condition, and marine survival of pink salmon in the area near PWS, Chapter 3 was a broader-scale study of the stability hypothesis. The stability hypothesis states that there is a 'window' at intermediate levels of light and nutrients where phytoplankton production is at its maximum (Gargett, 1997). Most of the GOA, where macronutrients are plentiful but primary production is limited through low light levels during part of the year, occupies the low-stability end of the optimal 'window.' The lower latitudes of British Columbia where upwelling dominates, light levels are higher and more uniform throughout the year but macronutrients are limited in the surface layer, occupies the high-stability end of the optimal 'window.' Within the coastal downwelling domain of the northeast Pacific Ocean, salmon survival should improve when water column stability within coastal regions increases, while water column stability should have the opposite effect on marine survival within the upwelling domain (Gargett, 1997).

Marine survival data in Chapter 3 originated from hatchery stocks ranging from Vancouver Island, British Columbia, to Kodiak Island, Alaska, with distinct northern (downwelling) and southern (upwelling) groups dividing above the Queen Charlotte Islands (Mueter *et al.,* 2002a). Since the dominant scale of covariation among the survival rates of pink salmon stocks is roughly 500 km (Pyper *et al.,* 2001), and the direction of ocean migration of pink salmon after they leave the hatchery is known (north/northwest) (Takagi *et al.,* 1981), hatcheries within similar regions were grouped together and individual stock survival rates were correlated with stability in one of four oceanographic regions in the direction of ocean migration. Linear mixed-effects models

combined parameters that were associated with the entire northeast Pacific pink salmon population (fixed effects) and parameters that were associated with individual pink salmon stocks (random effects). Several model forms for stability effects were investigated including no stability effects, a stability effect common to all stocks, a stability effect common to all stocks with random stock specific stability effects, stability effects varying by region, stability effects varying by region with random stock-specific stability effects, stability effects varying by domain (one or more regions combined), and stability effects varying by domain with random stock-specific stability effects.

The overall goal of this dissertation was to further understanding of how regional oceanographic processes, such as stability, affect the survival rate of juvenile salmon in upwelling and downwelling domains of the northeast Pacific. Further understanding of these regional oceanographic processes will lead to better management and better predictions of climate change effects on Pacific salmonids.

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Chapter 1: Relationship of water column stability and mixed layer depth to the growth, condition, and survival of pink salmon (*Oncorhynchus gorbuscha*) in the northern coastal Gulf of Alaska

ABSTRACT

The relationship between the environmental covariates water column stability and mixed layer depth (MLD) within two water masses, the Alaska Coastal Current (ACC) and shelf, and the growth and condition of several stocks of hatchery-reared and wild pink salmon (*Oncorhynchus gorbuscha*) in the northern Gulf of Alaska (GOA) with consideration of effects on marine survival was examined. It was hypothesized that pink salmon growth and condition have a positive relationship with summer water column stability. Contrary to expectation, neither stability nor year was statistically significant in explaining variability in fish growth rates, while year effects were important in explaining variability in fish condition within the ACC and shelf water masses. It was hypothesized that growth and condition have a negative relationship to the summer MLD. Results demonstrated that MLD was not statistically significant in explaining variability in growth rate or fish condition within either GOA water mass. It was also hypothesized that pink salmon survival has a positive relationship to condition and stability. Contrary to expectation, none of these relationships was statistically significant.

Key Words: condition, growth, Gulf of Alaska, mixed layer depth, *Oncorhynchus gorbuscha,* pink salmon, stability, survival, potential energy anomaly

INTRODUCTION

Salmon (genus *Oncorhynchus)* survival is strongly influenced by processes affecting their first year of life in the coastal ocean (Francis and Hare, 1994). Coastal conditions have a greater influence on survival rate and recruitment than large-scale climate patterns (Mueter *et al.*, 2002). Within the northern coastal Gulf of Alaska (GOA), earlier and stronger stratification with a shallower mixed layer depth (MLD) may be beneficial for juvenile salmon survival. Studies have linked increased water column stability to increased chlorophyll-*a* concentrations, longer bloom duration, and earlier onset of the spring bloom (Henson, 2007). During the winter and early spring in the northern coastal GOA, vertical mixing is not suppressed and macronutrients are plentiful since water column stability is low and the MLD is deep. Primary production is light limited, though, resulting in low overall production in the system. During the spring, solar radiation strengthens and warms the surface layers so that mixing is inhibited by the increase in the water column stability and shallowing of the MLD (Miller, 2004). With sufficient light levels, an increase in primary production during the spring bloom should lead to elevated secondary production and higher survival rates of salmon in the Gulf.

Pink salmon (*O. gorbuscha*) are the most abundant Pacific salmon in Alaskan waters and support a large commercial fishery (Heard, 2003). They are an integral part of the Prince William Sound (PWS) and Gulf ecosystems. Between mid-April and early June, wild pink salmon fry enter PWS coastal waters (Cooney, 1993). Around May, PWS hatcheries release their pink salmon fry to assure they overlap with the timing of the spring zooplankton bloom (Cooney *et al.,* 1995). Juveniles released during the peak of the *Neocalanus* and *Calanus* spp. spring bloom have higher survival rates than those released after the bloom, due to higher growth rates and a greater body mass from the large abundance of food (Cooney *et al.,* 1995; Beauchamp *et al.,* 2007). By July or early August, juveniles migrate out of PWS waters into the coastal GOA where they are distributed across the entire shelf in surface waters (upper 10-20 m) (Welch *et al.,* 2003).

The GOA shelf can be divided oceanographically and bathymetrically into three main regimes: the inner shelf regime or Alaska Costal Current (ACC) water mass, the middle shelf regime (shelf water mass), which lies between the inner and outer shelf regimes and is influenced by the more saline and nutrient rich Alaskan Stream, and the outer shelf/shelf break regime (shelf break water mass) (Weingartner, 2007). These three water masses are separated by frontal systems that have limited exchange of mass, material, and momentum among them (Weingartner, 2007). Of the three regimes, the inner shelf regime is particularly important for juvenile pink salmon.

The inner shelf water mass occurs in waters less than 50 km from the coast in the summertime and is mainly influenced by the low salinity, nutrient poor ACC. The migration band of juvenile pink salmon is influenced by the strength and location of the ACC, which can affect salmon production. A significant portion of the early growth for juvenile pink salmon occurs in the ACC over the continental shelf from July to October (Cooney, 1984).

Measures of both growth rate and body condition can be used as an indicator of habitat quality and to identify links between regional oceanographic conditions and juvenile salmon survival (Mueter *et al.,* 2002; Brodeur *et al.,* 2004). Growth and condition of other salmon species, such as coho (*O. kisutch*), have been shown to vary by oceanographic regime. In the northern California Current habitat quality assessed through juvenile coho growth and condition is better north of Cape Blanco (Brodeur *et al.*, 2004).

How oceanographic conditions within the GOA water masses affected the growth, condition, and ultimately the survival of pink salmon stocks originating from PWS was examined in this study. It was hypothesized that juvenile pink salmon growth and condition should have a positive relationship with summer water column stability and a negative relationship with the summer MLD. During the spring, solar radiation strengthens so that mixing is inhibited by the increase in the water column stability and shallowing of the MLD. With sufficient light levels, an increase in primary production during the spring bloom should lead to higher secondary production and higher survival

rates of salmon in the Gulf. It was also postulated that survival of hatchery pink salmon is positively related to fish growth, fish condition, and stability in the Gulf. As the fish growth rate increases or condition improves, the chance of survival and therefore the overall year-class survival should also improve. The influence of ocean conditions on marine survival should be strongly correlated with fish growth rate and fish condition (Brodeur *et al.,* 2004).

METHODS

Fish Samples

Wild and hatchery-reared juvenile pink salmon samples were collected within the northern coastal Gulf from July 8th to August 12th from 1998, and 2000 through 2004 (Fig. 1.1, Table 1.1). Samples were frozen at sea until analysis. The hatchery of origin of a fish can be identified based on examination of otolith thermal markings. Hatcheries include the Armin F. Koernig hatchery (AFK), the Cannery Creek hatchery (CCH), the Solomon Gulch hatchery (SGH), and the Wally Noerenberg hatchery (WNH). Unmarked fish were assumed to be of wild origin. Both fish length (measured as fork length in millimeters) and fish whole weight (measured in grams) were recorded after fish frozen at sea were later thawed. The fish sampled were considered representative of the overall population because they were sampled in mid-summer when most of the fish are still in the Sound and the northern coastal GOA.

A water mass category was assigned to each transect's stations where fish information was collected. These categories were assigned because salinity gradients can affect the distribution of forage fishes (Abookire and Piatt, 2005), pre-migration sea surface salinity can affect the survival of pink salmon fry (Mueter *et al.,* 2005), and different processes influence stratification on the inner and outer shelf (Weingartner, 2007). Oceanographic data were used to categorize each transect's stations based on salinity profiles in the upper 2 m of the water. The criterion used to designate a station by water mass or location was one of the following: Alaska Coastal Current water mass

(ACC) = salinity < 30 at 2 m depth or the mid-shelf water mass (shelf) = salinity ≥ 31.5 at 2 m depth.

Growth Rate

Thermal markings on otoliths allow each hatchery fish to be identified to a specific hatchery of origin, release date, and size at release. Using a subset of the fish samples, instantaneous fish growth rate (G) was estimated for all hatchery fish that could be assigned to a specific hatchery release date using the equation,

$$W_{C_i} = W_{R_j} e^{G_i t_i}; i = 1, \ldots, n, \quad (1.1)$$

where W_{C_i} is the weight at time of capture for an individual fish i, W_{R_j} is the weight at time of release for the release group j of which fish i is a member, and t is the number of days between release and capture for an individual fish (Ricker, 1975). This methodology has been used in many salmon growth studies (e.g., Willette, 1996; Brodeur *et al.*, 2004). As the initial weights of fish of wild origin were not known, growth rates for wild fish were not calculated. All fish from a hatchery release group (a release group shared the same release date and weight at release) captured in a single fish haul were treated as a single sample to avoid potential pseudoreplication (Hurlbert, 1984). Sample pseudoreplication occurs when multiple observations have been taken on a single replicate of a treatment, which can lead to an inappropriate inflation of the 'effective sample size,' underestimates of standard errors, and spurious statistical significance (Millar and Anderson, 2004).

Because release timing or release weights are not standardized across hatcheries, growth rate measurements were standardized by hatchery using each hatchery's mean growth rate and standard deviation (SD) in growth rate [standardized value=(X-mean)/SD]. Growth rates were first averaged for each year/hatchery combination so that all years contributed equally in the growth standardization. These values were again

averaged by hatchery to calculate a 'mean' and 'standard deviation' to be used in the 'standardized value' formula.

Tukey multiple comparison tests (Zar, 1999) were performed to determine if multiple groups of fish with distinct release dates and corresponding release weights for AFK and WNH fish differed in growth rates. Fish from different release groups were pooled if they were not significantly different (Table 1.2). For example, in 2001, WNH had three release dates, May 7th, May 17th, and May 17th, corresponding to release weights of 0.71 g., 0.69 g., and 0.70 g. Based on the multiple comparison tests, the two releases on May 17th were not significantly different but were significantly different than the May 7th release. Therefore, the May 17th releases were pooled and considered the WNH01 release group and the May 7th release was considered the WNH release group. After the appropriate release groups were pooled, each haul was averaged to calculate a standardized growth rate by release group and year within each water mass (Fig. 1.2). SGH had more than one fry release date in 1998, 2003, and 2004 but did not have unique thermal otolith marks for each release date; therefore SGH fish samples from these years were not used in any growth analyses (Table 1.2).

Condition Index

The study of fish condition is usually based on the analysis of weight-length data in the standard allometric equation,

$$W_{C_i} = (aL_{C_i})^b;\ i = 1, \ldots, n, \tag{1.2}$$

where W_{C_i} and L_{C_i} are the weight and length at time of capture for an individual fish i, respectively (Huxley and Tessier, 1936). The weight-length analysis assumes that heavier fish of a given length are in better condition. It is believed to be a good indicator of the general fitness of the population of fish under consideration. To estimate the a and b coefficients, measurements are log transformed to lineralize the equation. The data are

then fit by simple linear regression. The residuals from the back transformation of the measurements ($W_{C_i} - \widehat{W}_{C_i}$) are the condition index of the fish population.

Due to size-dependent growth in this study, the linearized standard allometric equation was not used to calculate fish condition (De Robertis and Williams, 2008). Instead, locally weighted regression scatterplot smoothing (LOWESS) models were fit with a range of smoothness parameters, f = 0.2 – 0.9. The advantage of this non-parametric method is that it is not sensitive to outliers. Model residuals from each of the LOWESS fits were examined to determine the proper smoothness parameter. As f increases, the smoothing curve becomes smoother. If the chosen f is too small, the curve will have a large variance, and if the chosen f is too large, there will be a large bias in the curve. The value of f was chosen by increasing the f parameter to the point where the residual graph began to show a pattern and then choosing a slightly smaller f parameter (Cleveland, 1979; Cleveland, 1985). The final LOWESS model was fit with a smoothness parameter of 0.75. A residual (condition) from the LOWESS model was calculated for each individual fish. If the value was positive (negative), the fish had a better (worse) condition than the average fish.

All fish from the same origin (individual hatchery or wild) captured in a single fish haul were considered a single sample to avoid potential pseudoreplication. A mean condition by origin (individual hatchery or wild) and year within each water mass was then calculated (Fig. 1.3).

Potential Energy Anomaly (Stability)

Hydrographic information was collected over a similar time period near or at stations where fish samples were collected in the northern coastal Gulf. Hydrographic samples were collected from June 27th to August 24th from 1998, and 2000 through 2004 (Fig. 1.1, Table 1.1). The oceanographic data stratified each transect's stations based on salinity profiles in the upper 2 m of the water column (ACC water mass, shelf water mass).

The upper water column stability or stratification (ϕ) was estimated for each station using the potential energy equation from Simpson *et al.*, (1977),

$$\phi = \frac{1}{h}\int_{-h}^{0}(\bar{\sigma}_\theta - \sigma_\theta)gzdz;\ \bar{\sigma}_\theta = \frac{1}{h}\int_{-h}^{0}\sigma_\theta dz\ \left(\mathrm{Jm^{-3}}\right);\ \sigma_\theta = \rho_{S,\theta,0} - 1000\ \mathrm{kg\ m^{-3}}. \quad (1.3)$$

The potential energy equation calculates the work required to bring about the vertical redistribution of the mass during complete mixing. A strongly stratified water column (more stable water column) requires more energy to mix than a weakly stratified water column. In equation 1.3, h is the water column depth, z is the vertical coordinate, g is the acceleration of gravity (9.81 m s^{-2}), and ρ is the density of sea water by depth (kg m^{-3}) calculated using salinity (S), potential temperature (θ), and atmospheric pressure. The variable σ_θ is the density of a water parcel when it has been removed adiabatically to the reference pressure 0 dbar. Units are in Joules per cubic meter. One meter depth intervals with a total depth of 100 m per hydrographic profile were used in the calculations. Each hydrographic profile was analyzed separately for stability. Any hydrographic profile missing more than nine sequential intervals was excluded. Stability was computed for a total of n=395 individual hydrographic profiles (157 in the ACC water mass and 238 in the shelf water mass).

Stability has a strong seasonal pattern in the GOA; it begins to increase in the spring and levels off in the summertime (Dobbins *et al.*, 2009). This is exemplified by water column stabilities (J m^{-3}) calculated using equation 1.3 from the long-term time series at oceanographic station GAK 1 (59° 50.7' N, 149° 28.0' W) (http://www.ims.uaf.edu/gak1/, accessed: July 1st, 2010) (Royer, 1982; Weingartner *et al.*, 2005) (Fig. 1.4). GAK 1 is located at the mouth of Resurrection Bay near Seward, Alaska and is the station closest to shore on the Seward Line transect of hydrographic stations. Temperature and salinity versus depth profiles have been taken at this oceanographic station since December 1970.

To remove the seasonal pattern in the data, LOWESS (Cleveland, 1979) models were used. LOWESS models were fit to all hydrographic profiles, separated by water mass, using a range of smoothness parameters, f=0.2–0.9. Depending on the cruise dates and sufficient water column samples, the range in dates of the water column samples varied each year (Table 1.1). Model residuals from each of the LOWESS fits were examined to determine the proper smoothness parameter (Cleveland, 1979; Cleveland, 1985). For the ACC water mass, a smoothing parameter of 0.70 was used. For the shelf water mass, a smoothing parameter of 0.80 was used.

Within each water mass, residuals from the LOWESS fits were then calculated for each hydrographic profile (Fig. 1.5). If the residual was positive (negative), the individual profile's stability was greater (less) than the average stability from the years 1998, and 2000 to 2004. Next, the average stability residual by year and water mass was calculated (Fig. 1.6). Stability in the ACC water mass had a larger variance (s^2=7119) than the shelf water mass (s^2=515). There was relatively good sampling coverage of stability over the late June to August time period from 2001 to 2003. Sampling coverage was towards the earlier time period in 1998 and 2004, and towards the later time period in 2000.

Mixed Layer Depth

The mixed layer depth is defined as the bottom of the quasi-homogenous region in the upper ocean where there is little change in density with depth. It is determined by a balance between destabilizing effects of mechanical mixing (tides and winds) and stabilizing effects of surface buoyancy flux (heat and freshwater) (Thomson and Fine, 2003). Turbulent mixing can easily overturn such a mixed layer. The larger the density difference across the bottom of the mixed layer and the larger the density gradient in the lower layer, the more stable the water column because turbulent mixing is suppressed and more energy is needed to mix the water column (Kara *et al.,* 2003). To determine the MLD, the split and merge algorithm was used (Pavlidis and Horowitz, 1974; Thomson and Fine, 2003; Sarkar *et al.,* 2005). This method is a computationally efficient and

flexible curve-fitting technique that estimates the optimal decomposition of plane curves and wave forms using piecewise polynomial functions.

In the split and merge algorithm, z_{min} was set at 10 m, z_{max} was set at 100 m, the error norm threshold for the first run was set at σ_1=0.1, and the error norm for the second run was set at σ_2=0.0.04 (R. Thomson, Institute of Ocean Sciences, Sidney, British Columbia, Canada, pers. comm.). A non-zero starting depth attempts to avoid effects of propwash and turbulent flow past the ship's hull (Thomson and Fine, 2003). Although a few MLDs could not be calculated, sampling coverage of the MLD over the summer time period (late June to late August) was similar to the sampling coverage of stability since the same hydrographic profiles were used (Fig. 1.5, Table 1.1). After the MLD was calculated for each hydrographic profile (152 in the ACC water mass, 230 in the shelf water mass), the average MLD by year and water mass was then calculated (Fig. 1.7).

Correlation Tests

Correlation tests were performed to determine relationships between stability and freshwater discharge. First, Spearman's rank correlation tests were performed between average summer stability residuals in the two different water masses from years 1998 and 2000 through 2004. Next, using the long-term time series at oceanographic station GAK 1 (Royer, 1982; Weingartner *et al.*, 2005), seasonal stabilities were calculated using equation 1.3 and compared to seasonal freshwater discharge (cubic m s^{-1}) from Southeast Alaska to Seward, Alaska (Royer, 1982) from 1990 to 2004.

Year-Class Survival

Survival was calculated as the ratio of the numbers of returning adults (returns to the hatchery plus harvest estimates) to smolts released one year earlier using estimates obtained from each hatchery of origin (AFK, CCH, SGH, or WNH) (Fig. 1.8). Since pink salmon have a two year life cycle, the fish sampled at sea in 1998, 2000 to 2004 were from eggs deposited one year earlier (the brood year), and each cohort returned as adults

one year later. Survival estimates were not available by release group or for wild fish during this time period.

For examining the relationship between stability and survival, the time series was extended by using summer oceanographic data from 1996 to 2004 from oceanographic station GAK 1 on the Seward Line transect. Water column samples from roughly the end of June to the end of August were used for calculating stability. An even longer time series of year-class survival was available, but not used because full thermal otolith marking of pink salmon to determine survival estimates was not done until 1997 (brood year 1995). Prior to that, coded wire tags were used (Joyce and Evans, 2001). Survival estimates from otoliths are higher than those from the coded-wire tag methods and have much narrower confidence intervals (Riffe and Mathisen, 2002).

After examining the residuals of different LOWESS fits, a LOWESS model was fit to GAK 1 summer stability data with a smoothness parameter of 0.8 (Fig. 1.9). Residuals from the LOWESS line were then calculated from each hydrographic profile. Each year had from n=2 to n=9 individual hydrographic profiles collected during the summer months, that extended from the surface to 100 m depth. Residuals from each year were then averaged.

STATISTICS

Growth Rate Models

The influence of stability and origin on the standardized growth rate from samples collected within the Gulf was evaluated using an analysis of covariance (ANCOVA). The most complicated model was

$$Z_i = \alpha + \beta_1 X_{i1} + \beta_2 X_{i1}^2 + \sum_{k=1}^{3} \gamma_k (D_{ik}) + \sum_{k=1}^{3} \delta_{1k} (X_{i1} D_{ik}) + \sum_{k=1}^{3} \delta_{2k} (X_{i1}^2 D_{ik}) + \varepsilon_i;\ i = 1, \ldots, n, \quad (1.4)$$

where Z_i represents the standardized growth rate observed in samples drawn from haul i, α is the intercept, X_{i1} and X_{i1}^2 are the quantitative regressors for the second order polynomial stability residuals, D_{ik} is a set of three indicator variables to represent the four hatcheries in the study, $(X_{i1}D_{ik})$ and $(X_{i1}^2D_{ik})$ are the interaction regressors, and ε_i is a random error term, $\varepsilon_i \sim N(0, \sigma_y^2)$. The parameters α, β_1, and β_2 are the polynomial coefficients for the reference group, the AFK hatchery, respectively. The coefficients for the other hatcheries are $(\alpha+\gamma_k)$ and $(\beta_1+\delta_{1k})$ + $(\beta_2+\delta_{2k})$, respectively. Separate analyses were run for data from each of the two water masses. Since the stability term, the MLD term, and the year term are collinear, the analysis was repeated, substituting year or average MLD for stability in a linear or quadratic model, respectively.

Using the maximum likelihood fits, models were compared using Akaike Information Criterion, corrected for small sample sizes (AICc),

$$\text{AICc} = n \ln(\text{RSS}) + \frac{2pn}{n-p-1}, \tag{1.5}$$

where n is the number of data points in the model, p is the number of estimated parameters, and RSS is the residual sum of squares of the fitted model. To determine the range of plausible models, the AICc score for each model was rescaled relative to the model with the lowest AICc value. Models with $\Delta \leq 2$ were considered equally plausible, while a model with $\Delta > 10$ was considered not competitive (Burnham and Anderson, 1998). Using the analysis of variance or analysis of covariance table, the terms in the equally competitive models were then tested for significance at the 5% level. If terms in the larger competitive model were significant, this model was chosen as the best, most parsimonious model.

Condition Index Models

The analysis of the influence of stability and origin on condition index was similar to that of the standardized growth rate (eq. 1.4) except an additional indicator was needed for the wild fish group. Separate analyses were run for data from each of the two water masses. The analyses were then repeated, substituting year or average MLD for stability in a linear or quadratic model, respectively. Models were also compared using AICc (eq. 1.5).

Year-Class Survival Models

To determine what factors might influence the survival of juvenile pink salmon, year-class survivals were compared to fish condition index using linear regression analysis. Year-class survival was regressed on the average fish condition during the prior year by hatchery, year, and water mass. Year-class survivals could not be compared to fish growth rates, since growth rates were analyzed based on release groups. Marine survival rates were only available on a yearly basis for each hatchery, not for each release group.

Using a Spearman's rank correlation test, the relationship between summer stability within the ACC water mass from station GAK 1 (1996 to 2004) and adult hatchery survivals, lagged one year, was also calculated.

Commonalities

In all analyses, evaluations of parallelism (same slope), coincidence (same intercept and slope), interactions, and influential outliers using Cook's distance and leverage measures, were done (Warren 1974; Cook 1977; Neter et al. 1996). To determine the aptness of the model fit and to determine any departures from the linear regression assumptions, diagnostics such as plots of the studentized residuals against year or against the fitted values were performed on the best fit model. To determine departures from normality for the error terms, both visual inspection of normal probability plots and the Shapiro-Wilks test were performed. The software used for the statistical analyses was the R language (http://cran.r-project.org). Preliminary analysis of the raw stability and fish datasets had

already omitted any potential outliers due to inaccurate data entries. While influential outliers were investigated, there was no basis for excluding the influential data points in any model fits except poor stability coverage over the time period or limited temporal coverage of fish samples. Therefore, unless specifically noted, influential outliers were not omitted from final model fits.

RESULTS

Correlation Tests

Summer stabilities within the ACC and shelf water masses in the northern coastal GOA were not correlated. Winter and spring stabilities within the ACC water mass, calculated from only station GAK 1, were positively correlated with freshwater discharge (Spearman's ρ=0.40, P=0.04, Spearman's ρ=0.58, P<0.001, respectively), the relationship with fall stabilities was negative (Spearman's ρ=-0.36, P=0.05), and there was no relationship in summer from 1990 to 2004.

Growth Rate Models

Contrary to expectation, stability, MLD, year, and hatchery did not explain the variability in fish growth rate within either the ACC or shelf water masses when all hatchery fish were included in the analysis. None of the competing models contained significant terms at the P=0.05 significance level or explained much of the variability in growth rate in either water mass (Table 1.3).

Condition Index Models

Contrary to expectation, only year explained the variability in condition index within both water masses (Table 1.4). Year explained 80% of the variability within the ACC water mass and 79% of the variability within the shelf water mass. There were departures from normality for the error terms in the model fit to the ACC water mass data due to heavy tails.

Most groups (CCH, SGH, WNH, and wild fish) showed similar interannual fluctuations in condition within both water masses (Fig. 1.3); fish condition was lower for years 1998, 2001 (except for CCH fish on the shelf) and 2003 and higher for years 2000, 2002, and 2004. The AFK hatchery fish deviated from this pattern in 2002; within the shelf water mass fish condition was low, and within the ACC water mass years 2002 and 2003 had very similar fish conditions (Fig. 1.3). Fish samples from cruises during year 1998 were only available from the Cape Puget transect from an OCC cruise that occurred around August 1st (Table 1.1). Due to the limited sampling area, the trend for 1998 may not be consistent with the entire northern coastal GOA sampling area for 1998.

Year-Class Survival Models

Contrary to expectation, survival had no clear relationship to fish condition within either the ACC or shelf water masses (Table 1.5). The relationship between summer ACC stability from station GAK 1 (1996 to 2004) and adult hatchery survivals (1997 to 2005 return years) was not statistically significant (Table 1.6).

DISCUSSION

Three hypotheses were tested in this study: the *stability hypothesis*, the *mixed layer depth hypothesis*, and the *survival hypothesis*. The *stability hypothesis* tested whether juvenile pink salmon growth rate and fish condition have a positive relationship with summer water column stability in the Gulf. Contrary to the hypotheses, neither stability nor year was statistically significant in explaining variability in fish growth rate within either the ACC or shelf water mass. While stability did not explain the variability in fish condition within the ACC or shelf water masses, year was statistically significant in both water masses.

Summer stabilities in the ACC and shelf water masses in the northern coastal GOA were not correlated in this study. Surface stratification begins adjacent to the coast in April or May in the inner shelf regime (Weingartner, 2007), then gradually spreads

offshore. Initiation of stratification in the ACC water mass is more complex and is driven by winds and coastal freshwater dispersal (Weingartner *et al.,* 2005), while initiation of stratification in the shelf water mass is driven by simpler one-dimensional processes of wind mixing and solar heating (Weingartner *et al.,* 2005; Weingartner, 2007). Except in late winter, stratification over the shelf water mass is always weaker than the ACC water mass (Weingartner, 2007).

Stratification occurs when buoyancy forces (freshwater and heating) are greater than mixing forces (tide and wind) (Henson, 2007); therefore, freshwater discharge and stability in the ACC water mass should be positively correlated. Station GAK 1 winter and spring stabilities were positively correlated with freshwater discharge, while the relationship with fall stabilities was negative, and there was no relationship in summer. The maximum coastal discharge is in the fall when precipitation is at its highest (Royer, 2005), yet the stability and discharge relationship was negative. This is most likely due to winds that begin to increase in the fall that act as destratifying processes. Average monthly downwelling wind speeds from Middleton Island on the northern GOA shelf begin to increase in August and are at a maximum in October (Weingartner *et al.*, 2005).

There have been a few prior studies linking water column stability and salmon survival in the southern regions (northern California/Oregon/Washington area), in the transitional regions (southern British Columbia, Canada), and in the northern regions (the Bering Sea, GOA) of the eastern North Pacific Ocean with mixed results. There is conflicting support in the southern regions. In the estuarine environment of Puget Sound, an optimal *mixing* 'window' was hypothesized, where fish-enhancing plankton production was highest during years with intermediate turbulent vertical mixing. Optimal phytoplankton conditions would result in higher growth rates, increased survival, and greater production of coho salmon off Washington (Pinnix, 1999). In a second test, cooler sea surface temperatures during the winter prior to smolt migration, which are associated with weaker spring stratification, lead to higher marine survival of Oregon coho salmon (Logerwell *et al.,* 2003). In a third test, coho salmon survival indices from Washington to

California were positively correlated with oceanographic and meteorological variables such as upwelling, cool sea surface temperatures, strong wind mixing, strong transport of the California Current, and a deep and weakly stratified upper mixed layer during the early marine period and during the return migration/overwintering period (Koslow *et al.*, 2002). Lastly, although water column stability was deemed important, the timing of ocean entry by coho salmon smolts in relation to the spring transition date was more critical to juvenile ocean survival off Washington (Ryding and Skalski, 1999).

There is no support for the *stability hypothesis* in the transitional regions. The *stability hypothesis* most likely failed off southern British Columbia, Canada, due to the transitional nature (mix of southern and northern influences) and estuarine influences of the area and the lack of a long-term time series of hydrographic information (Gargett *et al.,* 2001).

There is indirect support for the *stability hypothesis* in the northern regions. In the coastal GOA, increased water column stability was linked to increased chlorophyll-*a* concentrations, longer bloom duration, and earlier onset of the spring bloom (Henson, 2007), supporting a link between primary production and water column stability. Next, based on stability and zooplankton measurements in the Bering Sea, an optimal stability 'window' was hypothesized to exist on the eastern Bering Sea shelf. As stability increases past the 'optimal' level, post-bloom production on the middle shelf declines, large grazers cannot be supported, and there is a reorganization of the trophic levels present on the southeastern Bering Sea middle shelf. Relative to 1999, in 2004, the shelf zooplankton community shifted from large to small species, water column stability increased three-fold, and the diets of young-of-year walleye pollock (*Theragra chalcogramma*) shifted from large to small copepods (Coyle *et al.,* 2008).

The *mixed layer depth hypothesis* tested whether juvenile pink salmon growth rate and condition have a negative relationship with summer MLD in the GOA. MLD was not statistically significant in explaining variability in growth rate or fish condition within either water mass. Other studies have found that variability in salmon survival could be

explained by MLD. Although the seasons examined differed, a shallow MLD was associated with increased coho salmon survival both north and south of Vancouver Island (Hobday and Boehlert, 2001). South of Vancouver Island an increase in survival was associated with a shallow mixed layer depth at the time of smolt release. North of Vancouver Island an increase in survival was associated with a shallow mixed layer depth during the return migration (Hobday and Boehlert, 2001).

Mechanisms governing the effect of the MLD in a light-limited versus nutrient-limited region differ. In a light-limited downwelling domain, such as the GOA, a deeper mixed layer may decrease primary production by mixing cells out of the euphotic zone. In a nutrient-limited upwelling domain, such as northern California, Oregon, and Washington, a deeper mixed layer may increase primary production by resupplying nutrients from depth (Polovina *et al.,* 1995). When salmonids are present to consume the zooplankton, the optimal MLD for young salmonid survival is a depth that promotes an in-phase cycle between phytoplankton and zooplankton production (Parsons and Kessler, 1987). Therefore, the time period when the shallowing of the MLD is most important may differ for northern and southern regions. Aydin *et al.* (2005) hypothesized that MLD influences accelerated springtime growth in pink salmon in the eastern Subarctic gyre. Shallowing of the MLD during spring may concentrate zooplankton in the surface waters, reducing foraging costs for pink salmon. Although the Aydin *et al.* (2005) study was focusing on high-seas pink salmon growth, the mechanisms may be similar within inshore waters of the GOA. Therefore, it may be more appropriate to compare the PWS MLD during the springtime when the juveniles are released into the Sound with the fish growth rate and condition during the summer and subsequent survival the following year, rather than with the MLD in the summer.

There were limitations in this study. The main limitation dealt with seasonal variability in MLD. As seen in this study, during the summer months in the northern GOA, MLDs are relatively shallow with little variability (Sarkar *et al.*, 2005) (Fig. 1.7). From 1998 to 2004, the average MLD in the ACC water mass was 11.9 with a standard

deviation of 1.0 and the average MLD in the shelf water mass was 13.2 with a standard deviation of 2.7. In the winter and spring, MLDs have the greatest variability in the northern GOA (Sarkar *et al.*, 2005). In winter, high winds provide the energy to mix the water column, while cool temperatures and reduced freshwater discharge destabilize the water column contributing to the deepening of the mixed layer and replenishment of nutrients to the euphotic zone. The increase in solar radiation and freshwater runoff in the spring stabilizes the water column and shoals the MLD. Therefore, summer may not be the ideal season to detect annual variability in MLDs and to detect changes in fish condition and growth rate as a response to changing environmental conditions.

The *survival hypothesis* tested whether salmon survival is positively related to fish condition in the Gulf. Contrary to expectation, fish condition had no clear relationship to survival within either water mass. An individual's condition in one life stage may not directly relate to a survival advantage until a later life stage. Among and within Snake River Chinook salmon (*O. tshawytscha*) populations, fish condition, during the summer in their freshwater rearing habitats, was not strongly related to survival at downstream sites the following spring (Zabel and Achord, 2004).

Fluctuations in hatchery survival may stem from conditions prior to entering the coastal GOA, such as the timing of the PWS spring bloom, the PWS spring bloom intensity, or the timing of the onset of stability. An increased flow of oceanic zooplankton into PWS in 2002 may have contributed to high survival for this year class of juvenile pink salmon (Kline *et al.*, 2008). The spring phytoplankton bloom in PWS occurred earlier in 2000, 2002, and 2004, as compared to 2001 and 2003 (S. Henson, Princeton University, personal communication) (Fig. 1.10). The years 2000 and 2002 had a particularly early spring phytoplankton bloom peak on about days 106 and 111, respectively, as compared to those of 2001 and 2003 that occurred on about days 151 and 126, respectively (S. Henson, Princeton University, personal communication). Although all five years had similar maximum chlorophyll concentrations (4.8 to 5.4 mg m^{-3}), years 2000, 2002, and 2004 had chlorophyll concentrations that remained high for a longer

period, whereas the concentrations quickly dropped off in 2003. Compared to 2000 to 2004, the year 1998 had only a slight peak in chlorophyll concentrations on day 146. A more stable water column may have been responsible for the earlier, more intense spring blooms (Henson, 2007), higher fish condition for the CCH, WNH, SGH, and wild fish, and higher fish survival for the CCH, WNH, and SGH fish in 2000, 2002, and 2004.

If one assumed that the environment was constant, then fish condition at time of capture would only be an artifact of different hatchery-release conditions. However, the similar interannual fluctuations in condition for both hatchery and wild fish in this study support the contention that changes in the marine environment, rather than the fry condition at time of release, are influencing fish survival (Fig. 1.3). Other evidence stems from the Alaska Department of Fish and Game census of pre-emergent wild fry populations in index streams in PWS. A comparison of the wild return per fry density, which is a proxy for marine survival, with combined hatchery marine survivals from 1977 to 1995 showed similar fluctuations in survival for wild and hatchery fish (Cooney and Willette, 1997). An updated look at wild returns per fry versus hatchery survival would help strengthen or refute this hypothesis.

The fish of AFK hatchery did not follow the temporal patterns of survival and condition exhibited by other hatchery and wild fish; lower survivals and condition indices in 2001 and 2003, and higher survivals and condition indices in 2000, 2002, and 2004 (Figs 1.3 and 1.8). Both condition within the shelf water mass and year-class survival of the AFK hatchery fish decreased from 2001 through 2003 and survival in 2000 was lower than 2001. Similarly, Pyper *et al.* (2001) and Kline *et al.* (2008) found that the AFK hatchery survival did not co-vary with that of the other hatcheries, the aggregate hatchery survival, or the wild fish survival. These findings and the findings from this study may be due mainly to the location of the AFK hatchery (Fig. 1.1). The AFK hatchery is located on Evans Island and is the closest hatchery to the open water of the coastal GOA. Fish originating from SGH, WNH, and CCH must travel about 90 to 140 km to reach the coastal GOA (Willette *et al.,* 2001). Not only do the juveniles from the hatcheries within

PWS have a further distance to travel to the coastal GOA, but they may also reside in the Sound for approximately three to four months (Parker, 1997). Fry released from the AFK hatchery prefer the GOA-adjacent waters of Elrington Passage where they can persist for up to two months before outmigrating to the open ocean (Fig. 1.11) (Urquhart, 1979). The juveniles originating from the AFK hatchery most likely spend less time in the inner waters of PWS than the coastal GOA waters as compared to other hatchery and wild fish. Therefore, the AFK hatchery juveniles are more likely to be influenced by the ACC. An analysis of the spring/summer PWS stability, when the estuary hatchery juveniles reside there, may better reflect a connection between the estuary hatcheries and survival of returning adults the following spring.

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FIGURES

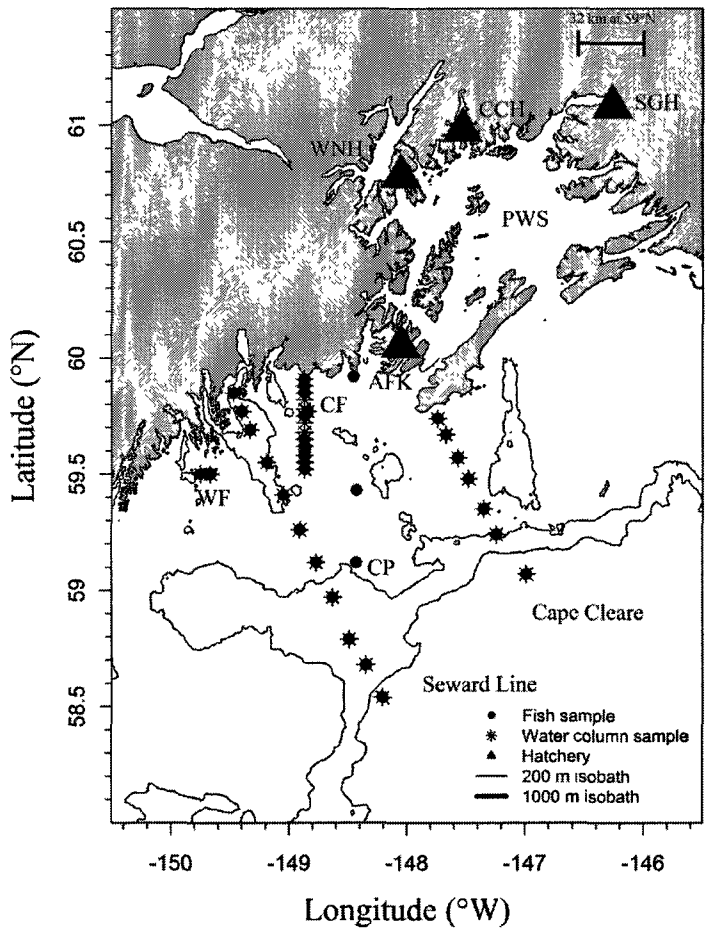

Figure 1.1 Stations in the central region of the northern coastal Gulf of Alaska where fish samples (filled circles) and/or water column samples (stars) were collected. The hatcheries are represented by the filled triangle symbol. Isobaths are shown at 200 m and 1,000 m. The main transects are labeled. CF: Cape Fairfield; CP: Cape Puget; WF: Western Front. Hatcheries are also labeled. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

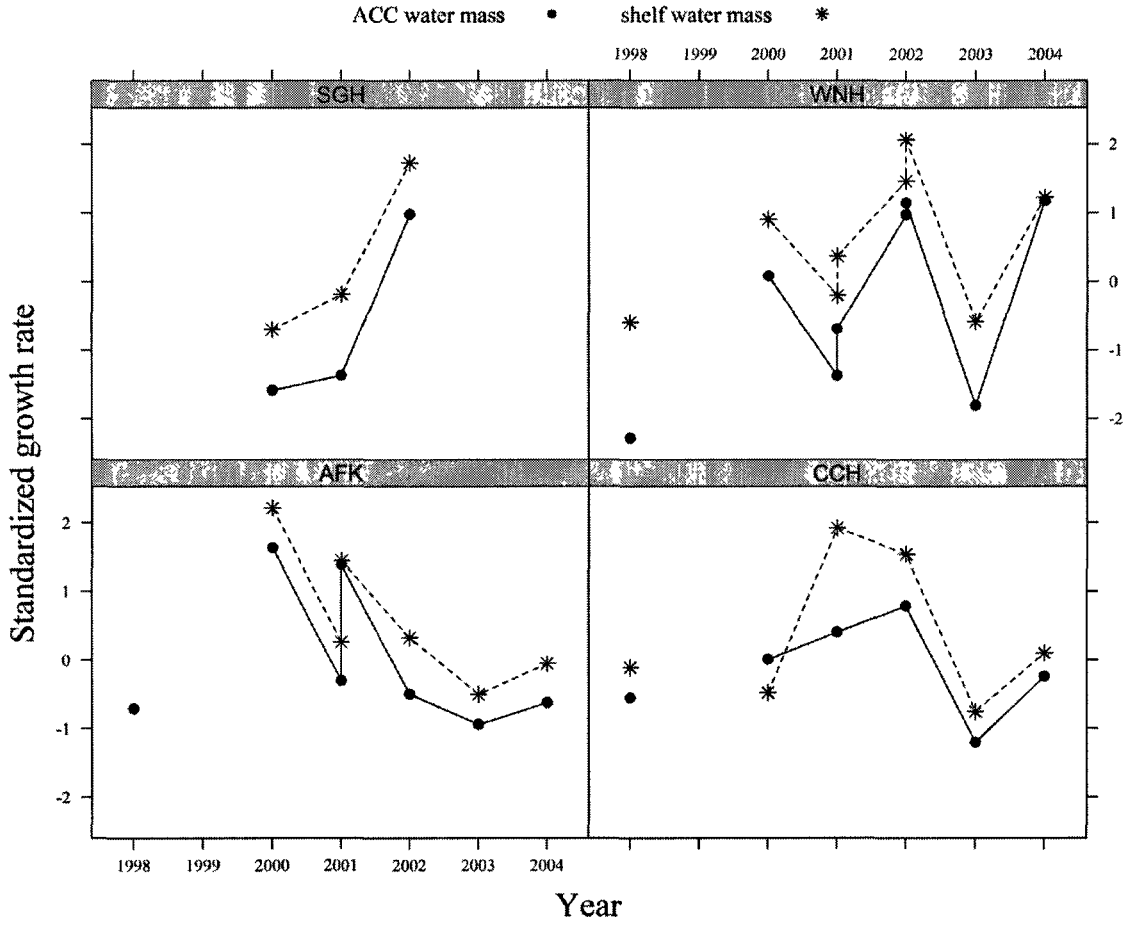

Figure 1.2 Standardized growth rate, by water mass, for hatchery fish from sampling years 1998, 2000 to 2004. The solid circles represent data collected from the Alaska Coastal Current (ACC) water mass and the stars represent data collected from the shelf water mass. There is more than one data point in 2001 for the fish from the Armin F. Koernig (AFK) hatchery and in 2001 and 2002 for the fish from the Wally Noerenberg hatchery (WNH) because there was more than one release group in those years based on Table 1.2. CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery

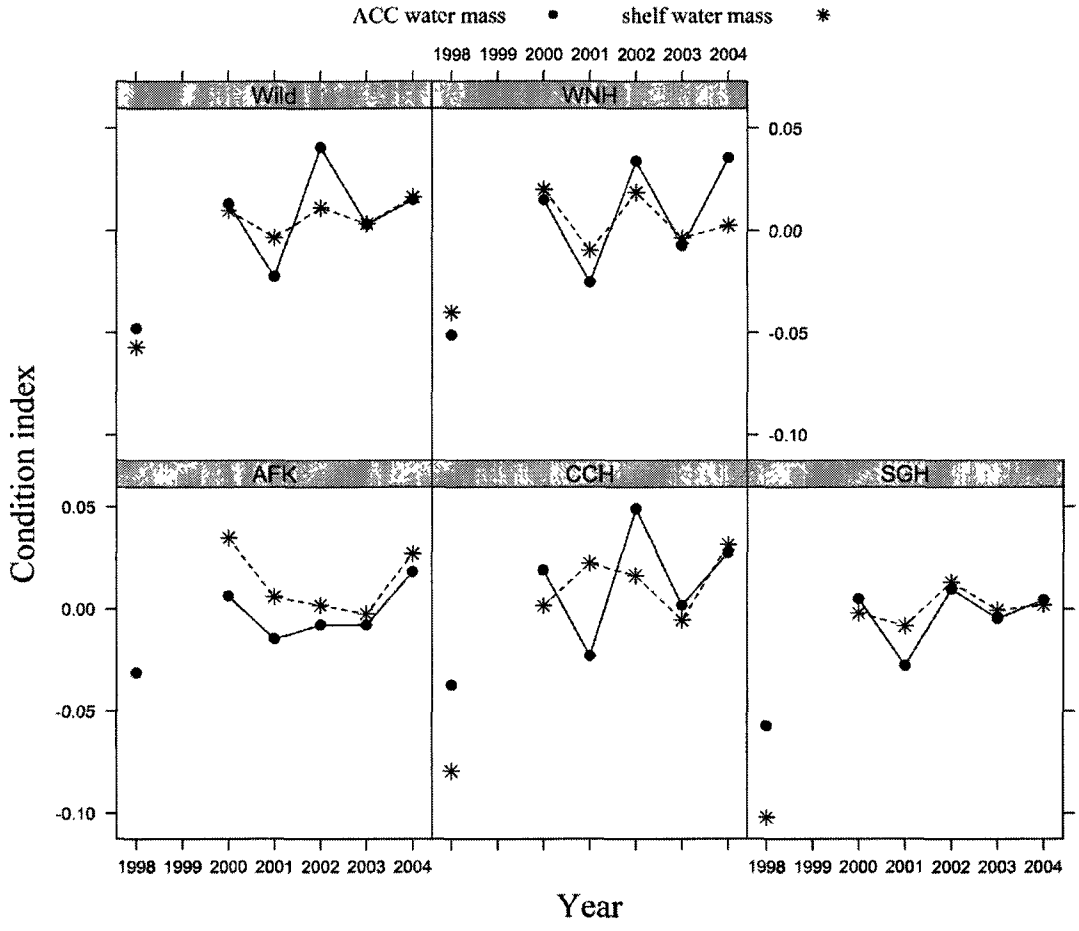

Figure 1.3 Fish condition, by water mass, for hatchery and wild fish from sampling years 1998, 2000 to 2004. The solid circles represent data collected from the Alaska Coastal Current (ACC) water mass and the stars represent data collected from the shelf water mass. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

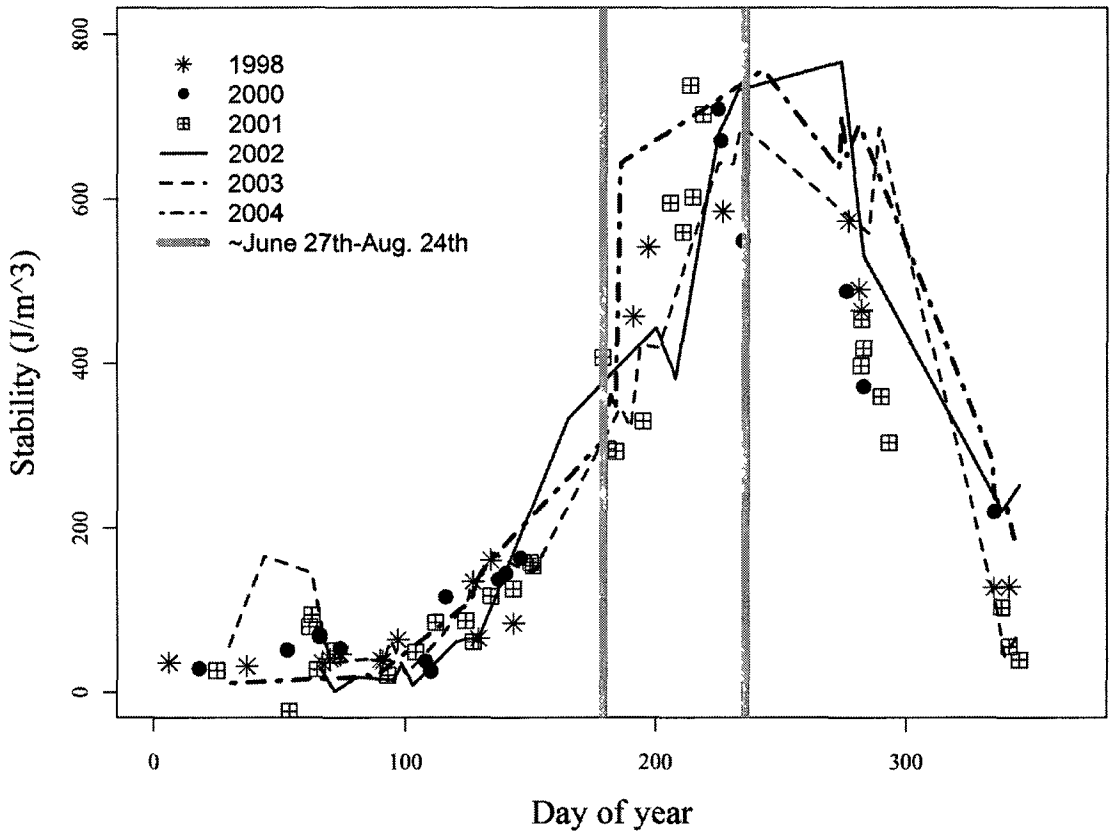

Figure 1.4 Stability throughout the year calculated from oceanographic station GAK 1 on the Seward line transect (http://www.ims.uaf.edu/gak1/) (Royer, 1982; Weingartner *et al.,* 2005). Each line represents a different year from 1998, 2000 to 2004. The two grey vertical lines show the summer season (~June 27th to August 24th) when juvenile pink salmon and water column samples were collected from the northern coastal Gulf of Alaska region

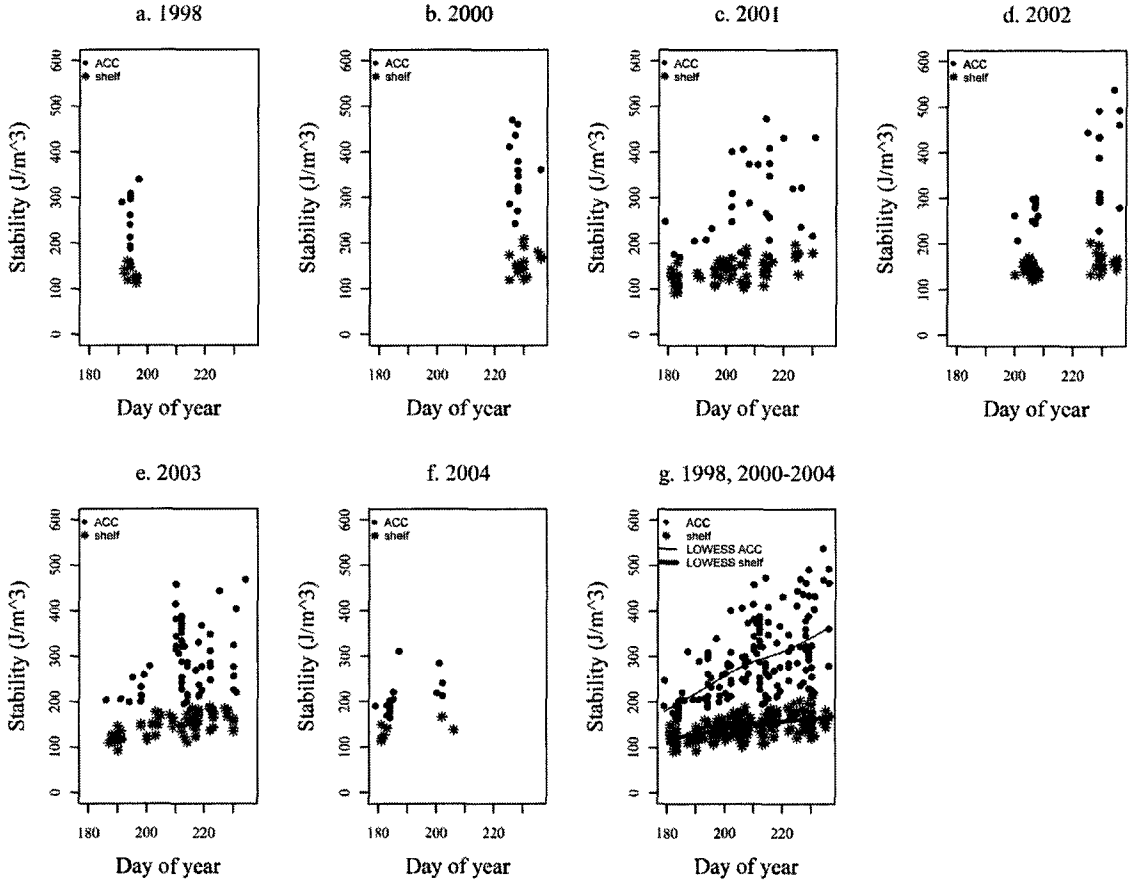

Figure 1.5 Individual water column stabilities by day of year (~June 27th to August 24th). The solid circles are from samples collected within the Alaska Coastal Current (ACC) water mass and the stars are from samples collected within the shelf water mass. In figure 'g,' the upper, lighter (lower, darker) line is the fit to all data points in the ACC water mass (shelf water mass). A smoothing parameter of 0.7 was used for the ACC water mass and a smoothing parameter of 0.8 was used for the shelf water mass.

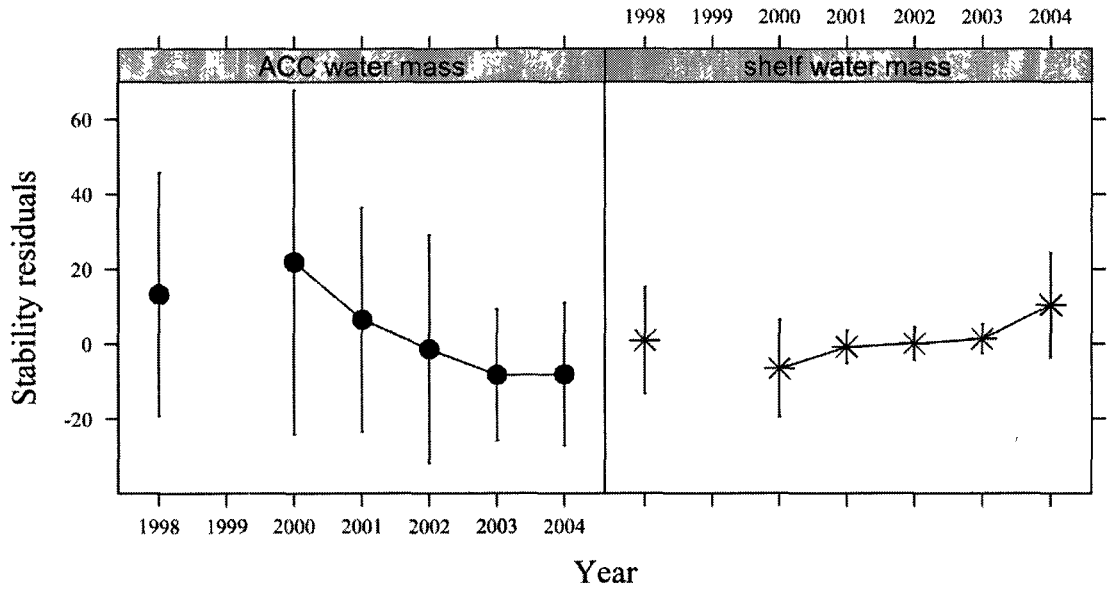

Figure 1.6 Average water column stability residuals by year (1998, 2000 to 2004) separated by water mass. Confidence intervals are shown by vertical lines.

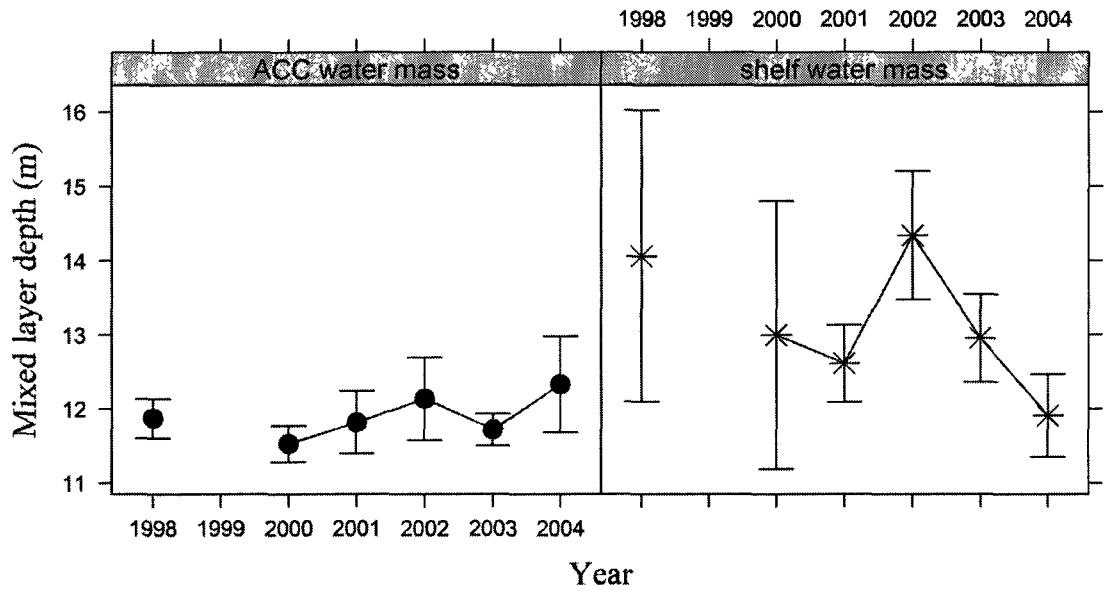

Figure 1.7 Average mixed layer depth by year (1998, 2000 to 2004) separated by water mass. Confidence intervals are shown by vertical lines

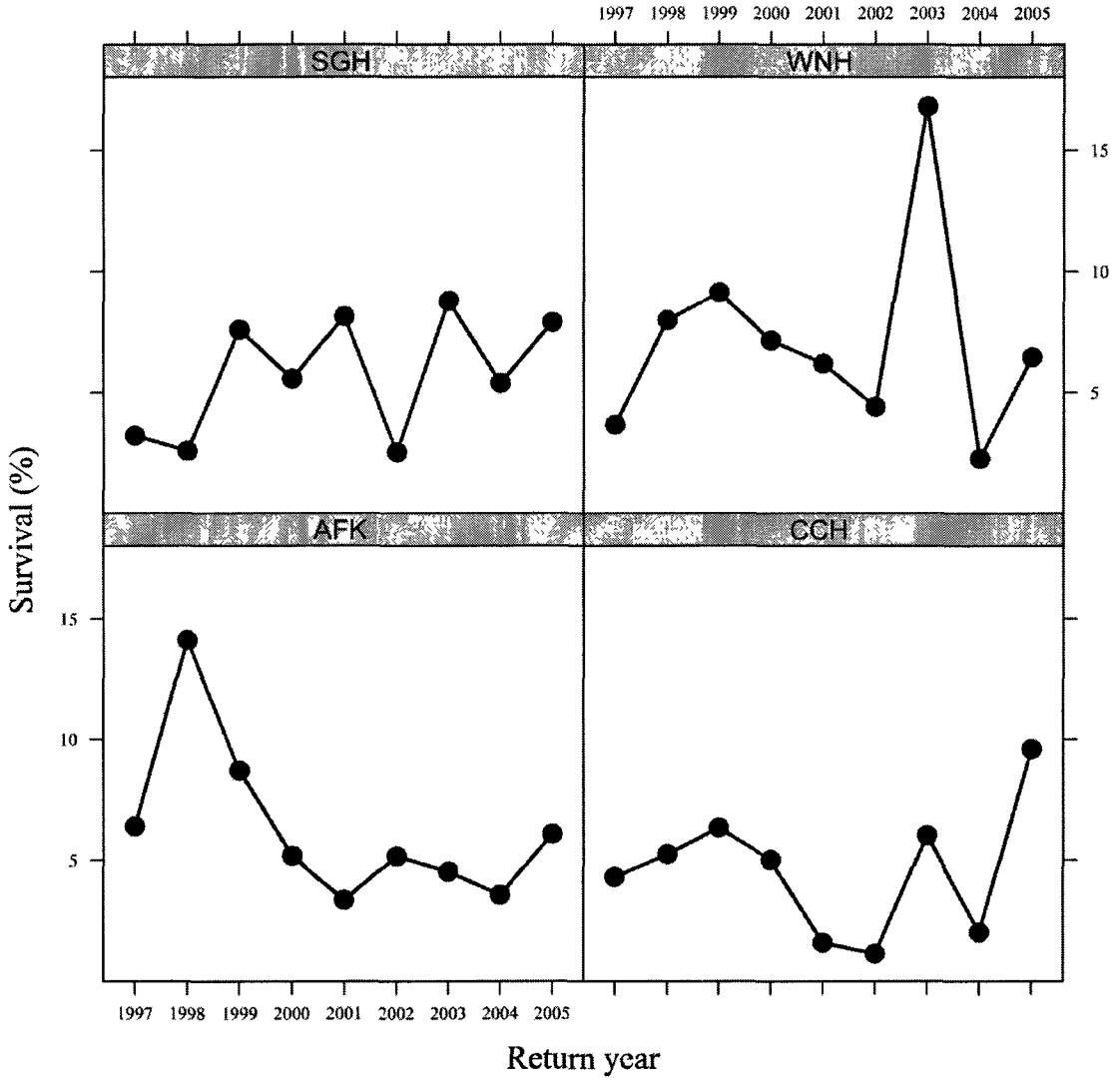

Figure 1.8 Comparison of fish survival by return year for the AFK, CCH, SGH, and WNH fish. Although return year 2000 (sampling year 1999) survivals are shown, these values were not used in all of the hypothesis tests because fish growth and condition data were not available from this year. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

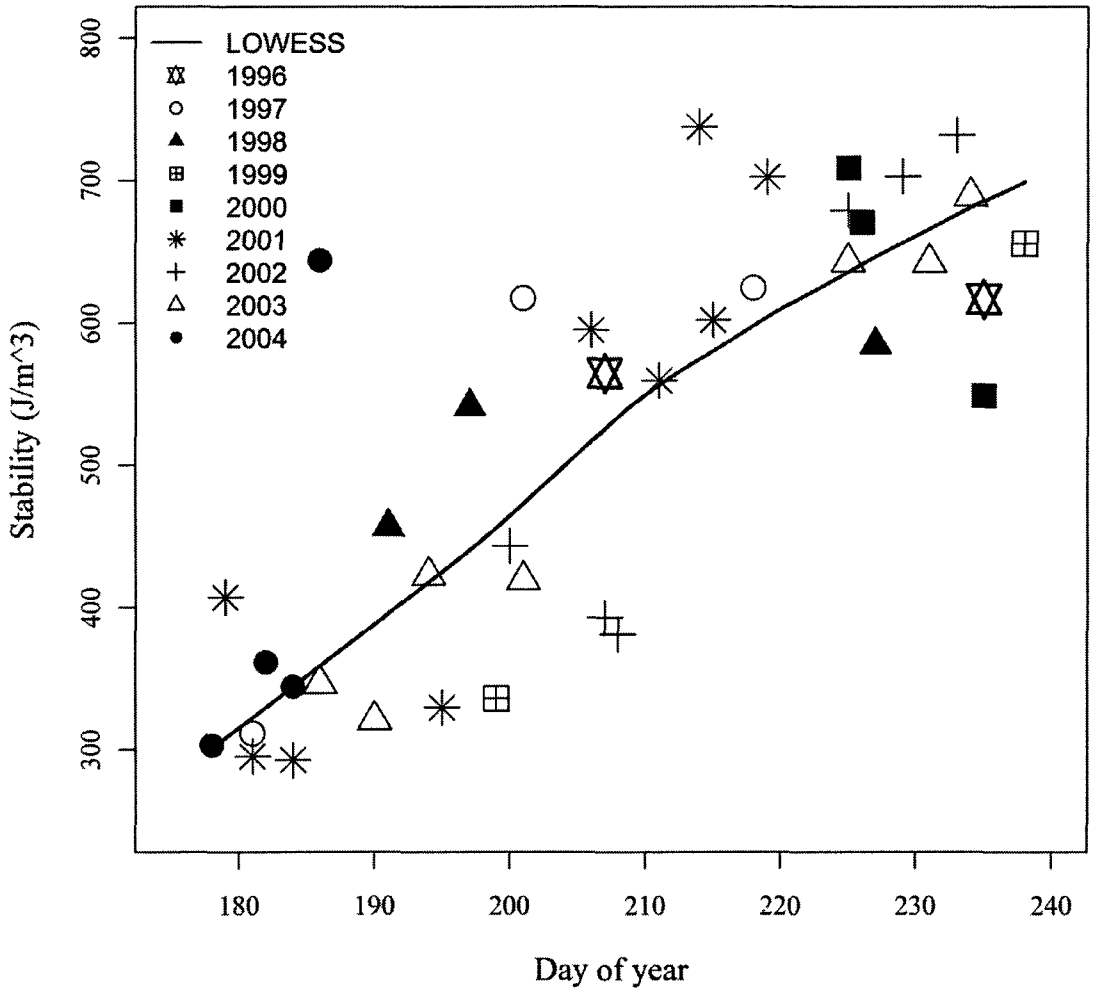

Figure 1.9 Individual water column stabilities from oceanographic station GAK 1 on the Seward Line transect (http://www.ims.uaf.edu/gak1/) (Royer, 1982; Weingartner *et al.*, 2005) and the LOWESS fit to all data points from ~June 27th to August 24th 1996 to 2004. A smoothing parameter of 0.8 was used.

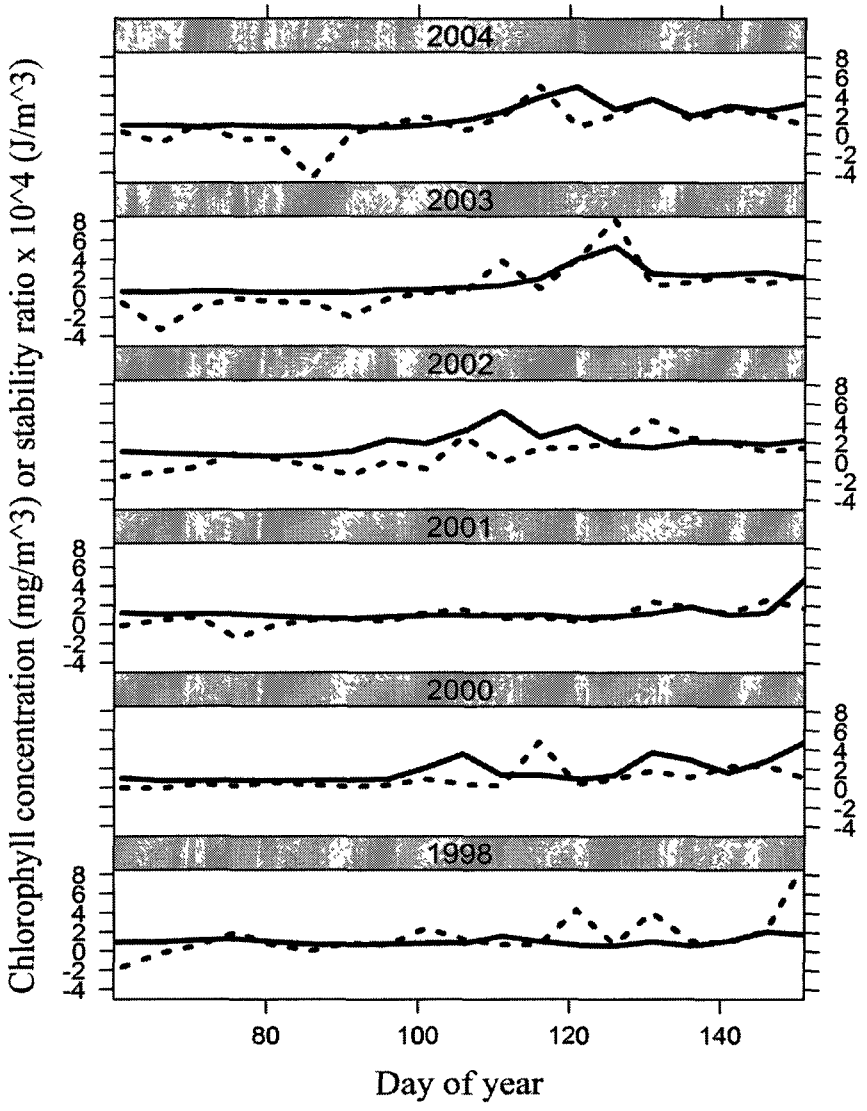

Figure 1.10 Chlorophyll concentration and the stability ratio by year collected near the mouth of Prince William Sound within the Alaska Coastal Current water mass (after Henson, 2007) from years 1998, 2000 to 2004. The solid line is the chlorophyll concentration and the dotted line represents the stability ratio.

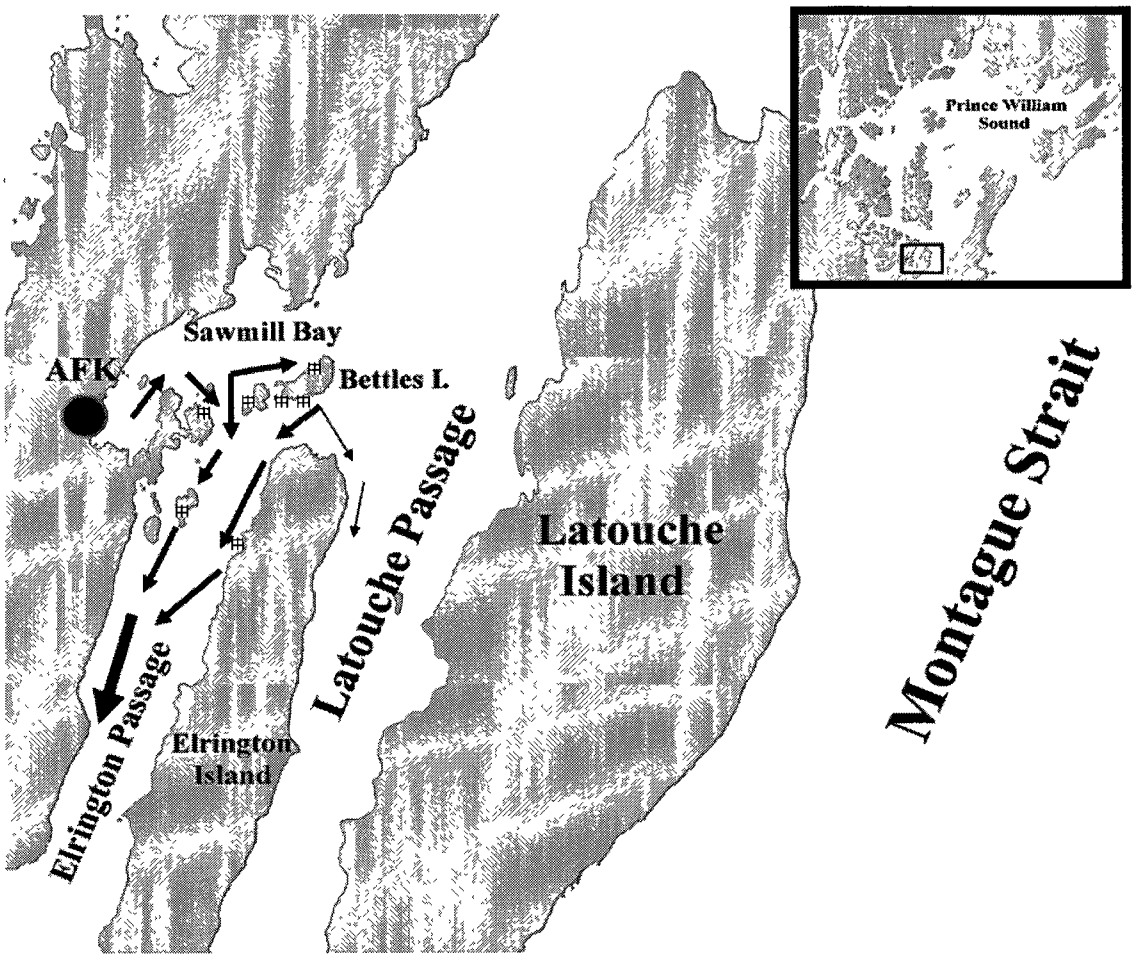

Figure 1.11 Major migration pathways (arrows) and fry nursery areas (squares with crosses inside) for hatchery pink salmon released from the Armin F. Koernig (AFK) hatchery. Data is based on a 1977, 1978 study (after Urquhart, 1979).

TABLES

Table 1.1 Range of sampling dates, separated by water mass (Alaska Coastal Current (ACC), shelf), for the hydrographic and fish samples.

Samples	Water mass	Year	Dates[c]	Water mass	Year	Dates[c]
Stability[a]	ACC	1998	7/10-7/16	shelf	1998	7/11-7/15
	ACC	2000	8/12-8/15, 8/23	shelf	2000	8/12-8/23
	ACC	2001	6/28-8/19	shelf	2001	6/30-8/4, 8/12-8/18
	ACC	2002	7/19-7/27, 8/13-8/24	shelf	2002	7/19-7/27, 8/14-8/23
	ACC	2003	7/5-8/22	shelf	2003	7/6-8/18
	ACC	2004	6/27-7/5, 7/18-7/20	shelf	2004	6/29-7/1, 7/20-7/24
Mixed layer depth[a]	ACC	1998	7/10-7/16	shelf	1998	7/11-7/15
	ACC	2000	8/12-8/15, 8/23	shelf	2000	8/12-8/23
	ACC	2001	6/28-8/19	shelf	2001	6/30-8/4, 8/12-8/18
	ACC	2002	7/19-7/27, 8/13-8/24	shelf	2002	7/19-7/27, 8/14-8/23
	ACC	2003	7/5-8/22	shelf	2003	7/6-8/18
	ACC	2004	6/27-7/5, 7/19-7/20	shelf	2004	6/29-7/1, 7/24
Juvenile pink salmon[b]	ACC	1998	8/1	shelf	1998	8/1
	ACC	2000	8/12	shelf	2000	8/12
	ACC	2001	7/8, 7/24-7/27	shelf	2001	7/9, 7/24-7/26
	ACC	2002	7/20-7/26	shelf	2002	7/22-7/25
	ACC	2003	7/13-719, 7/29-8/7	shelf	2003	7/27-8/5
	ACC	2004	7/20-7/23	shelf	2004	7/20-7/24

[a]The collections originated from: 1. the NOAA National Marine Fisheries Service Ocean Carrying Capacity Program (2000-2003), Jamal Moss and Ed Farley contacts, 2. the University of Alaska Fairbanks (UAF) U.S. Global Ocean Ecosystem Dynamics Northeast Pacific program (GLOBEC NEP) (2001-2004), 3. the Long Term Observation Program (LTOP) conducted by UAF (1998, 2000-2004), Russell Hopcroft and Tom Weingartner contacts, and 4. process-oriented projects (PROCESS) conducted by researchers from NOAA and several universities (2001, 2003), Suzanne Strom (Western Washington University), and Tom Weingartner (UAF Institute of Marine Science) contacts. The LTOP and PROCESS cruise data can be accessed at: http://globec.whoi.edu/jg/dir/globec/.

[b]The collections originated from two projects: the NOAA National Marine Fisheries Service Ocean Carrying Capacity Program (OCC) (1998, 2000-2003), Jamal Moss and Ed Farley contacts, and the University of Alaska Fairbanks (UAF) GLOBEC NEP (1998, 2000-2004). Length versus weight relationships observed in the two different projects (OCC and UAF) were similar, so the fish were considered to constitute one population and were pooled.

[c]Not every date was sampled within a given range.

Table 1.2 Year of release, release dates in May (unless specified), release group based on multiple comparison results for the four hatcheries (Armin F. Koernig Hatchery (AFK), Cannery Creek Hatchery (CCH), Solomon Gulch Hatchery (SGH), and Wally Noerenberg Hatchery (WNH)), average weight at time of release in grams based on release date, survival (percent of smolt to adult survival) by hatchery, and growth (percent body weight per day before standardization, separated by multiple comparison release groups) for hatchery pink salmon.

Release year	Hatchery	Release dates (May)	Release group[a]	Average release weight (g)	Survival (%)	Growth (% body weight per day)
1998	AFK	7, 21	AFK	0 45, 1 15	8 7	3 8
1998	CCH	30	CCH	0 36	6 3	5 8
1998	WNH	1, June 1	WNH	0 49, 1 72	9 1	3 7
2000	AFK	4, 24	AFK	0 39, 0 47	3 4	5 3
2000	CCH	June 8	CCH	0 34	1 6	5 9
2000	SGH	12	SGH	0 5	8 1	4 7
2000	WNH	16, 19	WNH	0 4, 0 5	6 2	4 7
2001	AFK	7, 23	AFK, AFK01	0 46, 0 48	5 2	4 2, 5 0
2001	CCH	31	CCH	0 32	1 1	6 7
2001	SGH	18	SGH	0 6	2 5	4 8
2001	WNH	7, 17, 17	WNH, WNH01, WNH01	0 71, 0 69, 0 70	4 4	4 1, 4 4, 4 4
2002	AFK	10, 25	AFK	0 43, 0 58	4 5	4 2
2002	CCH	31	CCH	0 39	6 0	6 9
2002	SGH	23	SGH	0 68	8 8	5 7
2002	WNH	10, 19	WNH, WNH02	0 6, 0 69	16 8	5 0, 5 2
2003	AFK	1, 12, 19	AFK	0 68, 0 97, 1	3 6	3 7
2003	CCH	31	CCH	0 68	2 0	5 4
2003	WNH	1, 7, 14	WNH	0 74, 0 85, 1 09	2 3	3 9
2004	AFK	6, 20, 20	AFK	0 54, 0 72, 0 66	6 1	3 9
2004	CCH	20	CCH	0 37	9 6	6 0
2004	WNH	7, 20, 20	WNH	0 58, 0 73, 0 59	6 5	5 0

[a]If more than one release group is stated, then there were significant differences between fish of different release dates and release weights and the fish were not pooled. Hatcheries may have had more release groups, but only the sampled release groups are listed.

Table 1.3 Comparison of models for the fish variable standardized growth rate. The term 'origin' represents the four hatchery groups. The abbreviation '*p*' stands for estimated number of parameters, 'RSS' is the residual sum of squares of the fitted model, and 'adj R^2' is the adjusted R squared value.

			Gulf of Alaska (ACC) [a]			*Gulf of Alaska (shelf)* [b]		
Model	Terms	*p*	RSS	ΔAICc	adj R^2	RSS	ΔAICc	adj R^2
1	$Stab^2$, Origin, $Stab^2$ x Origin	13	17.5	46.7	0.21	12.9	49.8	0.19
2	$Stab^2$, Origin	7	26.7	15.4	0.23	21.2	16.2	0.26
3	$Stab^2$	4	27.8	5.5	0.09	21.6	5.5	0.09
4	Stab, Origin, Stab x Origin	9	19.9	18.2	0.03	17.0	21.6	0.15
5	Stab, Origin	6	26.8	11.4	0.16	21.2	12.0	0.19
6	Stab	3	27.8	2.6	0.05	21.6	2.5	0.04
7	Origin	5	26.8	7.8	0.11	21.4	8.5	0.14
8	Year, Origin	10	13.5	15.0	0.26	11.1	18.2	0.20
9	Year	7	16.8	4.3	0.23	12.2	3.6	0.27
10	MLD^2, Origin, MLD^2 x Origin	13	11.2	36.0	0.23	13.5	50.8	0.24
11	MLD^2, Origin	7	23.2	12.1	0.07	18.1	12.6	0.07
12	MLD^2	4	24.2	2.2	0.05	18.5	1.9	0.06
13	MLD, Origin, MLD x Origin	9	16.0	13.1	0.17	18.0	22.9	0.21
14	MLD, Origin	6	24.7	9.5	0.07	19.8	10.5	0.11
15	MLD	3	25.7	0.7	0.04	20.4	1.2	0.02
16	Null model	2	27.8	0.0	NA	21.8	0.0	NA

[a] n=24, [b] n=23

Table 1.4 Comparison of models for the fish variable condition index. The term 'origin' represents the four hatchery groups and the wild group. The abbreviation '*p*' stands for estimated number of parameters, 'RSS' is the residual sum of squares of the fitted model, and 'adj R^2' is the adjusted R squared value.

			Gulf of Alaska (ACC) [a]			*Gulf of Alaska (shelf)* [b]		
Model	Terms	*p*	RSS	ΔAICc	adj R^2	RSS	ΔAICc	adj R^2
1	$Stab^2$, Origin, $Stab^2$ x Origin	16	0.0136	95.0	0.20	0.0192	98.8	0.44
2	$Stab^2$, Origin	8	0.0139	44.6	0.20	0.0197	45.4	0.06
3	$Stab^2$	4	0.0150	33.7	0.26	0.0219	34.9	0.12
4	Stab, Origin, Stab x Origin	11	0.0181	66.4	0.20	0.0238	65.2	0.31
5	Stab, Origin	7	0.0183	49.2	0.01	0.0242	47.5	0.10
6	Stab	3	0.0195	38.8	0.08	0.0267	37.9	0.03
7	Origin	6	0.0208	49.5	0.10	0.0243	44.1	0.06
8	Year, Origin	11	0.0024	6.1	0.84	0.0037	11.0	0.80
9	Year	7	0.0036	0.0	0.80	0.0047	0.0	0.79
10	MLD^2, Origin, MLD^2 x Origin	16	0.0102	86.3	0.10	0.0187	98.0	0.40
11	MLD^2, Origin	8	0.0108	37.1	0.38	0.0200	45.9	0.05
12	MLD^2	4	0.0120	26.9	0.41	0.0221	35.1	0.11
13	MLD, Origin, MLD x Origin	11	0.0180	66.2	0.19	0.0192	59.0	0.06
14	MLD, Origin	7	0.0184	49.4	0.02	0.0204	42.5	0.07
15	MLD	3	0.0196	39.0	0.07	0.0224	32.8	0.13
16	Null model	2	0.0219	39.9	NA	0.0267	35.5	NA

[a] n=30, [b] n=29

Table 1.5 Summary of the best fit models for year-class survival.

	Coefficient	Standard error
Dependent variable: **Year-class survival**	R^2_{adj}=-0.0091, F=0.7918 on 1 and 22 d.f., P=0.3832	
Gulf of Alaska (ACC)		
Intercept	6.0560	0.7050
Condition	23.4130	26.3120
Dependent variable: **Year-class survival**	R^2_{adj}=-0.0461, F=0.0304 on 1 and 21 d.f., P=0.8632	
Gulf of Alaska (shelf)		
Intercept	5.8592	0.7367
Condition	-4.0489	23.2133

Table 1.6 Results of the Spearman's rank correlation test.

Hatchery	Spearman's ρ	P
AFK	0.62	0.09
CCH	-0.27	0.49
SGH	0.37	0.34
WNH	0.05	0.91

Chapter 2: Relationship of water column stability to the growth, condition, and survival of pink salmon (*Oncorhynchus gorbuscha*) in the northern coastal Gulf of Alaska and Prince William Sound[1]

Abstract

The relationship between water column stability and the growth, condition, and marine survival of several stocks of pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound (PWS) and two water masses, the Alaska Coastal Current (ACC) and shelf, in the northern coastal Gulf of Alaska (GOA) was examined. For fish sampled within PWS, stability during early marine residence explained less than 5% of the variability in fish growth, and the relationship was not the same for all stocks. While the relationship was negative for fish from the Armin F. Koernig, Solomon Gulch, and Wally Noerenberg hatcheries, the relationship was positive for fish from the Cannery Creek hatchery. Contrary to expectation, stability just prior to fish capture was not statistically significant in explaining variability in fish condition within PWS or within either GOA water mass. Cohorts with individuals heavier at a given length sampled during the year of release within the ACC water mass experienced higher survival during the return year, the following spring. When stability was below average just prior to capture within PWS, the relationship between condition index and year-class survival was positive; when stability was above average just prior to capture within PWS, the relationship between condition and year-class survival was negative.

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[1]Miller, S.E., M.D. Adkison, and L. Haldorson. 2011. Relationship of water column stability to the growth, condition, and survival of pink salmon (*Oncorhynchus gorbuscha*) in the northern coastal Gulf of Alaska and Prince William Sound. Prepared for submission to the Canadian Journal of Fisheries and Aquatic Sciences.

Introduction

Of the seven species of Pacific salmon, early marine mortality may be most important to pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon. Unlike the other species that spend from one to three years in freshwater rearing habitats, pink and chum salmon have short freshwater life stages. The small, vulnerable fry migrate directly to the ocean soon after hatching (Heard 1998; Salo 1998). Between mid-April and early June wild pink salmon fry enter Prince William Sound (PWS) coastal waters (Cooney 1993) and around May, hatcheries release their pink salmon fry into the estuary. To maximize growth rates during this early marine period, wild salmon fry migration may be coupled with the timing of the large calanoid copepod spring bloom, as hatchery-reared fry released during the peak of the bloom have higher survival rates than those released after the bloom (Cooney et al. 1995). During this zooplankton bloom there is an overlap between the surface distribution of feeding juvenile pink salmon and Pacific herring (*Clupea pallasii*) and walleye pollock (*Theragra chalcogramma*), which also feed on large calanoid copepods and prey on juvenile fish (Willette et al. 1999).

During these first few weeks of marine life in PWS, juvenile pink salmon inhabit shallow, coastal areas (Cooney et al. 1981) where early marine mortality is dominated by predation. There is a tradeoff between remaining in the coastal refugia and venturing offshore, where both foraging success and predator abundance increase. Rapid growth aided by plentiful food resources tends to minimize mortality risk because the faster-growing juveniles are vulnerable to predators for a shorter amount of time (Parker 1971; Healey 1982). Studies of juvenile pink salmon in PWS using back-calculated size and growth measurements determined from the radius of scale circuli have found faster growth during high survival years (Moss et al. 2005; Cross et al. 2008).

While the initial period of early marine mortality is focused on predation pressure, the second main period of early marine mortality is based on a physiological response. Juveniles failing to reach a critical body size by the end of their first summer may not have the energy reserves to survive the over-wintering period (Beamish and Mahnken

2001). Body condition is a measure of this nutritional state or relative "fatness" of an organism and is an index of a fish's ability to survive times of resource scarcity (Millar and Hickling 1990). Therefore, body condition is thought to be positively related to fitness, survival, and reproductive output (Jakob et al. 1996). While the measured growth rate reflects the overall history of foraging success and metabolic response to environmental conditions (Mason et al. 1995), body condition is more reflective of the more recent environment the fish experienced.

During early marine residence, wild and hatchery-reared juvenile pink salmon spend from two to four months within the Sound (Urquhart 1979; Parker 1997). A slower and weaker development of ocean stratification with a deeper mixed layer depth may be more beneficial for juvenile pink salmon survival in PWS (Eslinger et al. 2001). During cooler, stormier springs, phytoplankton blooms are prolonged and do not intensify as quickly due to the presence of a deeper mixed layer. Through periodic interruptions from increased winds remixing the water column and resupplying nutrients to the surface, phytoplankton production is lengthened, the interaction between phytoplankton and the springtime zooplankton community is prolonged, and more organic matter is retained in pelagic food webs (Eslinger et al. 2001). In shallow embayments of the Alaska coastal fjord environment, specific primary production rates have been found to peak on average 14 to 28 days after the spring bloom initiates (Ziemann et al. 1991). The annual peak in zooplankton biomass, which lags primary production by one to two months, provides food for juvenile salmon and salmon prey (Cooney 1988; Boldt and Haldorson 2003). By July or early August, juveniles migrate out of the estuary into the coastal waters of the Gulf of Alaska (GOA).

The oceanographic processes that affect early marine mortality are believed to be quite different in the Gulf (Cooney 1993). While slower and weaker development of stratification with a deeper mixed layer depth may enhance juvenile pink salmon survival in the Sound, earlier and stronger stratification with a shallower mixed layer depth may be more beneficial within the northern coastal Gulf (Eslinger et al. 2001; Henson 2007).

Studies have linked increased water column stability to increased chlolophyll-*a* concentrations, longer bloom duration, and earlier onset of the spring bloom (Henson 2007). During the winter and early spring, vertical mixing is not suppressed and macronutrients are plentiful since water column stability is low and the mixed layer depth is deep. Primary production is light-limited, though, resulting in low overall production in the system. During the spring, solar radiation strengthens and warms the surface layers so that mixing is inhibited by the increase in the water column stability and the shallowing of the mixed layer depth (Miller 2004). With sufficient light levels, an increase in primary production during the spring bloom should lead to elevated secondary production and higher survival rates of salmon in the GOA.

During the summer months, juvenile pink salmon are distributed across the entire GOA continental shelf in surface waters (upper 10-20 m), but are rarely found past the shelf break (Welch et al. 2003). The shelf can be divided oceanographically and bathymetrically into three main water masses: the inner shelf water mass or Alaska Costal Current (ACC) water mass, where a significant portion of the early juvenile growth occurs between July and October (Cooney 1984); the middle shelf water mass (shelf water mass); and the shelf break water mass (Weingartner 2007). These three water masses are separated by frontal systems which limit exchange (Weingartner 2007).

Measures of growth rate and body condition can be used to indicate habitat quality and to identify links between regional oceanographic conditions and juvenile salmon survival (Mueter et al. 2002; Brodeur et al. 2004). In the northern California Current, habitat quality assessed through juvenile coho salmon (*O. kisutch*) growth and condition is better north of Cape Blanco (Brodeur et al. 2004). After their first summer in the marine environment, the connection between ocean conditions and marine survival of sockeye salmon (*O. nerka*) on the eastern Bering Sea shelf is likely through the juvenile salmon size and condition. Juvenile sockeye salmon grow larger, are in better condition, and have increased marine survival during warmer oceanographic regimes due to an increase in prey abundance of mainly age-0 walleye pollock (Farley et al. 2007). For

reared Atlantic salmon (*Salmo salar)* in the Baltic Sea, there is a combined influence of both smolt size and mean July sea surface temperature on survival. Larger smolts had higher survival rates, and higher sea surface temperatures within the migration area increased the survival of young salmon (Kallio-Nyberg et al. 2004).

Since pink salmon have a short life cycle and non-overlapping year classes, they are an ideal species to study the effects of oceanographic conditions on marine survival. How oceanographic conditions within the Sound and the Gulf water masses affected the growth, condition, and ultimately the survival of pink salmon stocks originating from PWS was examined in this study. For the first part of the *stability hypothesis,* it was postulated that growth rate and fish condition should increase with decreasing stability within PWS. In contrast, it was postulated that fish condition should increase with increasing stability within the northern coastal Gulf. For the *survival hypothesis,* it was postulated that fish condition and environmental factors, such as water column stability, should predict year-class survival for juvenile pink salmon.

Methods

Fish Samples

Wild and hatchery-reared juvenile pink salmon samples were collected within the Sound from June 17th to September 20th in years 1998 through 2004 and within the northern coastal Gulf from July 8th to October 9th in years 1997 through 2004 (Figs 2.1 and 2.2, Table 2.1). The hatchery of origin was identified based on examination of otolith thermal markings; hatcheries include the Armin F. Koernig hatchery (AFK), Cannery Creek hatchery (CCH), Solomon Gulch hatchery (SGH), and Wally Noerenberg hatchery (WNH). Unmarked fish were assumed to be of wild origin. A water-mass category was assigned to each transect's stations where fish information was collected. These categories were assigned because salinity gradients can affect the distribution of forage fishes (Abookire and Piatt 2005), pre-migration sea surface salinity can affect the survival of pink salmon fry (Mueter et al. 2005), and different processes influence

stratification on the inner and outer GOA shelf (Weingartner 2007). Oceanographic data were used to categorize each transect's stations based on salinity profiles in the upper 2 m of the water. The criteria used to designate a station by water mass were: Alaska Coastal Current water mass (ACC) = salinity < 30 at 2 m depth and located in the northern coastal GOA, the mid-shelf water mass (shelf) = salinity $\geq$ 31.5 at 2 m depth and located in the northern coastal GOA, or PWS (stations located within PWS). Stations within PWS had a salinity range of 19.39 to 31.94.

Growth Rate

Thermal markings on otoliths allow each hatchery fish to be identified to a specific hatchery of origin, release date, and size at release. Using a subset of the fish samples, fish growth rate was estimated for all hatchery fish sampled within PWS that could be assigned to a specific hatchery release date, and for which stability information was available within two weeks before the hatchery release date to within two weeks after the hatchery release date (Table 2.1). Although growth rate reflects the overall life history of a fish, the juveniles are traveling between different water masses, and thus different stability environments, from release to capture. Fish captured in the GOA shelf water mass, for example, have experienced three different water masses and thus different stabilities within each water mass they encounter during their juvenile migration to the open ocean. It was not feasible to quantify the amount of time the individual fish spent in each water mass during its summer migration and then compare the fish's growth to the water mass and the water mass's stability. Therefore, it was only feasible to examine growth rates for fish captured within PWS. These rates were compared to the aggregated stability residuals within two weeks before the hatchery release date to within two weeks after the hatchery release date. Growth rate was not examined for fish sampled within the ACC or shelf water masses.

Fish growth rate (G) was estimated using the equation,

(2.1) $W_{C_i} = W_{R_j} e^{G_i t_i}; i = 1, \ldots, n.$

In equation 2.1, W_{C_i} is the weight at time of capture for an individual fish i, W_{R_j} is the weight at time of release for the release group j of which fish i is a member, and t is the number of days between release and capture for an individual fish (Ricker 1975). This methodology has been used in many salmon growth studies (e.g., Willette 1996; Brodeur et al. 2004). As the initial weight of wild fish was not known, growth rates for wild fish were not calculated.

Sample pseudoreplication occurs when multiple observations have been taken on a single replicate of a treatment (Hurlbert 1984). This can lead to an inappropriate inflation of the 'effective sample size,' underestimates of standard errors, and spurious statistical significance (Millar and Anderson 2004). All fish from a hatchery release group (a release group shared the same release date and weight at release) captured in a single fish haul were treated as a single sample to avoid potential pseudoreplication; if fewer than five fish from a release group were taken in the haul, data for that group were not used. Although WNH had two releases on May 17th, 2001, the release weights only differed by 0.01 grams; therefore these two releases were treated as a single release (Table 2.2).

Because release timing or release weights are not standardized across hatcheries, growth rate measurements were standardized (Z_i) by hatchery,

(2.2) $Z_i = \frac{G_i - \bar{x}_k}{s_k}; k = \text{hatchery}.$

Growth rates were first averaged for each year/hatchery combination so that all years contributed equally in the growth standardization. The mean ($\bar{x}_k$) and standard deviation(s_k) by hatchery, for use in equation 2.2, were then calculated using the annual averages for each hatchery.

Since fish of the same release group caught together are usually more similar than those in the general population, fish collected in clusters will contain less information about a population attribute than individual fish sampled randomly. Therefore, to calculate the confidence bounds around the yearly standardized growth rates, the ratio estimator $\hat{R}$ of the mean standardized growth rate was used,

(2.3) $\hat{R}_{yj} = \frac{\sum_{i=1}^{n} M_i \hat{\mu}_i}{\sum_{i=1}^{n} M_i}$; $\hat{R}_{yj} \pm t_{0.05(2),n-1}\, s_{\hat{R}}$; y=year, j=release group,

where M_i is the number of fish, by release group, measured for growth rate at haul i, $\hat{\mu}_i$ is the average standardized growth rate of fish in haul i, and $s_{\hat{R}}$ is the standard deviation of the ratio estimator (Pennington et al. 2002) (Fig. 2.3). For each release group, a ratio estimator was calculated by year. Confidence intervals were not calculated unless there were at least three hauls sampled for a given release group in a year. The software used for the statistical analyses was the R language with the package 'fishmethods' (http://cran.r-project.org).

Condition Index

Fish condition represents the weight of an individual fish compared to an average fish of the same length and is thought to reflect the recent foraging history. Using a subset of the fish samples, fish condition indices were estimated for all hatchery and wild fish for which stability information was available within the two weeks immediately prior to the sample collection within the water mass in which it was collected (Table 2.1).

Due to size-dependent growth, the residuals of the back-transformation of the weight measurements calculated from the linearized standard allometric model were not used to calculate condition index (De Robertis and Williams 2008). Instead, locally weighted regression scatterplot smoothing (LOWESS) models were fit with a smoothness parameter of 0.85. The value of f was chosen by increasing the f parameter to the point where the residual graph began to show a pattern and then choosing a slightly smaller f

parameter (Cleveland 1979; Cleveland 1985). A residual (condition index) from the LOWESS fit was calculated for each individual fish. Fish were separated into five groups of origin (by hatchery or wild). To avoid potential pseudoreplication, characteristics of all fish from each group of origin taken in a haul were averaged; if fewer than five fish from a group were taken in the haul, data for that group were not used.

Since fish of the same hatchery caught together are usually more similar than those in the general population, the ratio estimator,

(2.4) $\hat{R}_{yl} = \frac{\sum_{i=1}^{n} M_i \hat{\mu}_i}{\sum_{i=1}^{n} M_i}$; $\hat{R}_{yl} \pm t_{0.05(2),n-1}\, s_{\hat{R}}$; y=year, l=origin,

was used to calculate the confidence bounds around the yearly fish condition (Pennington et al. 2002) (Figs 2.4 to 2.6). In this case, M_i is the number of fish, by origin, measured for condition at haul i, $\hat{\mu}_i$ is the average condition of fish in haul i, and $s_{\hat{R}}$ is the standard deviation of the ratio estimator (Pennington et al. 2002). For each hatchery or wild group l, a ratio estimator was calculated by year. Confidence intervals were not calculated unless there were at least three hauls sampled for a given hatchery or for wild fish in a year.

Year-Class Survival

Using estimates obtained from each hatchery (AFK, CCH, SGH, or WNH), survival was calculated as the ratio of the number of returning adults (escapement plus harvest estimates) to smolts released one year earlier (S.D. Moffitt, Alaska Department of Fish and Game, Area Research Biologist, personal communication, 2010). Estimates from brood years 1996 to 2003, when all hatchery-produced pink salmon from PWS had thermal otolith marks, were used (Joyce and Evans 2001). Since pink salmon have a two-year life cycle, the fish sampled at sea in 1997 through 2004 were from eggs deposited one year earlier (the brood year), and each cohort returned as adults one year later (1998

to 2005). Survival estimates were not available by release group or for wild fish during this time period.

Potential Energy Anomaly (Stability)

Hydrographic information was collected over a similar time period near or at stations where fish samples were collected in PWS and in the northern coastal GOA (Figs 2.1 and 2.2). Hydrographic samples were collected from April 18th to October 23rd in years 1998 through 2004 in PWS and from June 27th to October 22nd in years 1997 through 2004 in the northern coastal GOA. The upper water column stability or stratification (ϕ) was estimated for each station using the potential energy equation from Simpson et al. (1977),

$$(2.5)\quad \phi = \frac{1}{h}\int_{-h}^{0}(\bar{\sigma}_\theta - \sigma_\theta)gz\,dz;\ \bar{\sigma}_\theta = \frac{1}{h}\int_{-h}^{0}\sigma_\theta\,dz\ \left(\mathrm{Jm^{-3}}\right);\ \sigma_\theta = \rho_{S,\theta,0} - 1000\ \mathrm{kg\ m^{-3}}.$$

The potential energy equation calculates the work required to bring about the vertical redistribution of the mass during complete mixing. A strongly stratified water column (more stable water column) requires more energy to mix than a weakly stratified water column. In equation 2.5, h is the water column depth, z is the vertical coordinate, g is the acceleration of gravity (9.81 m s^{-2}), and ρ is the density of sea water by depth (kg m^{-3}) calculated using salinity (S), potential temperature (θ), and atmospheric pressure (Stewart 2007). The variable σ_θ is the density of a water parcel when it has been removed adiabatically to the reference pressure 0 dbar. Units for the potential energy anomaly equation are in Joules per cubic meter. One meter depth intervals over a depth range from 1 to 100 m were used in the calculation. Stability was calculated separately for each hydrographic profile. Any hydrographic profile missing more than nine sequential intervals was excluded. Stability was computed for a total of n=1344 individual hydrographic profiles, (481 in the ACC water mass, 473 in the shelf water mass, and 390 in PWS).

Stability has a strong seasonal pattern in the northern GOA; it begins to increase in the spring and levels off in the summer (Dobbins et al. 2009). To remove the seasonal pattern, LOWESS models were fit to all hydrographic samples, separated by water mass, using a range of smoothness parameters (0.2 – 0.9). Model residuals from each of the LOWESS fits were examined to determine the proper smoothness parameter (Cleveland 1979; Cleveland 1985). A smoothing parameter of 0.70 was used for the ACC water mass, 0.75 for the shelf water mass, and 0.45 for PWS (Fig. 2.7). Residuals from the LOWESS fits were then calculated for each hydrographic sample. If the residual was positive (negative), the stability of the individual sample was greater (less) than the average stability across all years, by water mass.

Statistics

Growth Rate Models

The influence of stability and origin on the standardized growth rate, from samples collected within PWS only, was evaluated using an analysis of covariance (ANCOVA). The most complicated model was

$$(2.6)\ Z_i = \alpha + \beta_1 X_{i1} + \beta_2 X_{i1}^2 + \sum_{k=1}^{3} \gamma_k (D_{ik}) + \sum_{k=1}^{3} \delta_{1k} (X_{i1} D_{ik}) + \sum_{k=1}^{3} \delta_{2k} (X_{i1}^2 D_{ik}) + \varepsilon_i; i = 1, \ldots, n,$$

where Z_i represents the standardized growth rate observed in samples drawn from haul i, α is the intercept, X_{i1} and X_{i1}^2 are the quantitative regressors for the second order polynomial stability residuals within two weeks before the hatchery release date to two weeks after the hatchery release date, D_{ik} is a set of three indicator variables to represent the four hatcheries in the study, $(X_{i1} D_{ik})$ and $(X_{i1}^2 D_{ik})$ are the interaction regressors, and ε_i is a random error term, $\varepsilon_i \sim N(0, \sigma_y^2)$. The parameters α, β_1, and β_2 are the polynomial coefficients for the reference group, the AFK hatchery, respectively. The coefficients for the other hatcheries are $(\alpha + \gamma_k)$, $(\beta_1 + \delta_{1k})$, and $(\beta_2 + \delta_{2k})$, respectively. Since the stability

term and the year term are collinear, the analysis was repeated, substituting year for stability in a linear model.

Condition Index Models

The analysis of the influence of stability and origin on condition index was similar to that of the standardized growth rate (eq. 2.6) except an additional indicator was needed for the wild fish group, and the stability data (X_i) was the average residual from the two weeks immediately prior to each sample collection. Separate analyses were run for data from each of the three water masses. The analyses were then repeated, substituting year for stability in a linear model.

Year-Class Survival Models

To determine what factors might influence the survival of juvenile pink salmon, year-class survivals were compared to stability residuals and to fish condition index, as well as interaction terms (eq. 2.7),

(2.7) $S_i = \alpha + \beta_1 X_{i1} + \beta_2 X_{i1}^2 + \beta_3 X_{i2} + \beta_4 X_{i2}^2 + \beta_5 X_{i1} X_{i2} + \beta_6 X_{i1}^2 X_{i2} + \beta_7 X_{i1} X_{i2}^2 + \beta_8 X_{i1}^2 X_{i2}^2 + \varepsilon_i; i = 1, \ldots, n.$

In equation 2.7, X_{i1} and X_{i1}^2 are the quantitative regressors for the second order polynomial stability residuals, X_{i2} and X_{i2}^2 are the quantitative regressors for the second order polynomial condition indices, and ε_i is a random error term, $\varepsilon_i \sim N(0, \sigma_y^2)$. Separate analyses were preformed for data collected within each of the three water masses.

Since marine survival rates were only available on a yearly basis for each hatchery (i.e., separate survival rates applying to fish sampled during different time periods or habitats could not be determined), data were aggregated over hatchery and year before statistical analysis. For example, there were six hauls of fish sampled within PWS from the Cannery Creek hatchery from July 7th to Aug. 16th, 2001. The condition

indices of fish from the six hauls were averaged, with each haul receiving equal weight, to calculate the average condition in year 2001 for CCH fish sampled within PWS. To compare survival to the most appropriate measure of stability, stability residuals from two weeks prior to the first recapture to the day of the last recapture in the same water mass and year were averaged. Therefore, all available stability residuals from June 23rd to Aug. 16th, 2001 collected within PWS were averaged to then compare to the year-class survival of CCH fish.

Year-class survivals could not be compared to fish growth rates and their corresponding stability residuals within PWS, since growth rates were analyzed based on release groups. Marine survival rates were only available on a yearly basis for each hatchery, not for each release group.

Commonalities

In all analyses, evaluations of parallelism (same slope), coincidence (same intercept and slope), interactions, and influential outliers using Cook's distance and leverage measures, were done (Warren 1974; Cook 1977; Neter et al. 1996). Significant interactions between continuous covariates were further tested with multiple linear regression (MLR) two-way interaction tools (Preacher et al. 2006). Preliminary analysis of the raw stability and fish datasets had already omitted any potential outliers due to inaccurate data entries. While influential outliers were investigated, there was no basis for excluding the influential data points in any model fits except poor stability coverage over the time period or limited temporal coverage of fish samples. Therefore, unless specifically noted, influential outliers were not omitted from final model fits.

Using the maximum likelihood fits, models were compared using Akaike Information Criterion, corrected for small sample sizes (AICc),

$$(2.8)\quad \mathrm{AICc} = n\ln(\mathrm{RSS}) + \frac{2pn}{n-p-1},$$

where n is the number of data points in the model, p is the number of estimated parameters, and RSS is the residual sum of squares of the fitted model. To determine the range of plausible models, the AICc score for each model was rescaled relative to the model with the lowest AICc value. Models with $\Delta \leq 2$ were considered equally plausible, while a model with $\Delta > 10$ was considered not competitive (Burnham and Anderson 1998). Using the analysis of variance or analysis of covariance table, the terms in the equally competitive models were then tested for significance at the 5% level. If terms in the larger competitive model were significant, this model was chosen as the best, most parsimonious model.

To determine the aptness of the model fit and to determine any departures from the linear regression assumptions, diagnostics such as plots of the studentized residuals against year or against the fitted values were performed on the best fit model. To determine departures from normality for the error terms, both visual inspection of normal probability plots and the Shapiro-Wilks test were performed. The software used for the statistical analyses was the R language (http://cran.r-project.org).

Results

Growth Rate Models

There were two competing models. One model contained linear stability effects, hatchery effects, and an interaction (model 4), and the other model contained the term year (model 10) (Table 2.3). Model 4 explained about 4% of the variability in growth rate and model 10 explained about 3% of the variability in growth rate within the Sound. Because the effect of stability varies by hatchery, stability and hatchery interact in affecting growth rate, and separate intercepts and separate slopes by hatchery are needed (Table 2.4). Each line in figure 2.8 represents the relationship of growth rate and stability by hatchery. While the relationship between stability and growth rate was negative for the fish from AFK, SGH, and WNH, matching prior expectation, the relationship was positive for fish from CCH (Fig. 2.8). The model fit the data from SGH poorly. Fish

originating from SGH exhibited a much more variable growth rate than those from other hatcheries, and data on these fish were only available for two years, both of which had above-average stability; this combination resulted in high leverage for several samples from SGH (Fig. 2.8c). In addition, the value of stability for one of these years may have been poorly determined; in the two weeks prior to release of SGH fish in 2000, there were 19 stability samples collected, but all were collected on only 2 of the 14 days, May 24th and May 25th. Nonetheless, the SGH data were retained.

Overall, neither of the best models, model 4 nor model 10, explained much (<5%) of the variability in growth rate and there were departures from normality for the error terms due to heavy tails in both models.

Condition Index Models

Neither linear nor quadratic stability effects were statistically significant within PWS, the ACC water mass, or the shelf water mass, although year and origin effects were important in some water masses (Figs 2.9 to 2.11, Table 2.5). Although there were three competing models in the PWS water mass, none of the stability models (model 3, model 6) contained significant terms at the P=0.05 significance level and these models explained <5% of the variability in condition index. Therefore, the best model within the PWS water mass was the null model (model 11).

Year effects were important within the ACC and shelf water masses, while origin effects were only important within the ACC water mass (Table 2.5). Year and origin explained about 31% of the variability in the condition index of fish collected within the ACC water mass (model 9) (Fig. 2.5). Year alone explained about 27% of the variability in the condition index of fish collected within the shelf water mass (model 10) (Fig. 2.6). There were no departures from normality for the error terms in the model fit to the ACC water mass data and only a slight departure from normality for the model fit to the shelf water mass data due to heavy tails.

Year-Class Survival Models

While neither condition index nor stability just prior to capture were important in the shelf water mass, condition index was important within the ACC water mass (model 12), and stability and condition effects were important within PWS (model 4) (Table 2.6). Interactions were only statistically significant within PWS. Although there were three competing models using the data collected from the shelf water mass (models 11, 12, 13), none of the models contained significant terms at the P=0.05 significance level and these models explained less than 2% of the variability in year-class survival. Therefore, the null model was preferred (model 13).

As expected, year-class survival and condition index had a positive relationship within the ACC water mass; cohorts with individuals heavier at a given length sampled during the year of release experienced higher marine survival (Fig. 2.12). Body condition explained about 31% of the variation in year-class survival within the ACC water mass (Table 2.7). In the model fit to the ACC water mass data, there were departures from normality for the error terms, where the error distribution was positively skewed.

The relationship within PWS was more complicated. There was only one competing model using all the data from the PWS water mass (n=18). The terms in the full model (model 1; results not shown), which included an interaction effect between a quadratic stability term and a quadratic condition index term, were significant. This model was originally chosen as the best model fit. This model explained about 89% of the variability in year-class survival, but had four influential outliers: WNH fish from year 2002, SGH fish from year 2004, and CCH fish from years 1998 and 2004. The samples from the Solomon Gulch hatchery had a particularly high Cook's distance. These samples were associated with a particularly low stability compared to the average. Although SGH fish hauls were collected within PWS on July 21st, 2004 and thus stability would be averaged from July 7th to July 21st in 2004, only one stability sample was available. This hydrographic sample was collected on July 21st and had below-average stability for this time of year in PWS. The residual of this sample was -120. Therefore,

this data point was excluded based on limited stability data. The Wally Noerenberg hatchery had a particularly high survival in 2002 (0.168) compared to the average hatchery survivals. Therefore, this data point was also excluded.

With the exclusion of the two data points, the best fit model using the data from PWS contained stability and condition effects with an interaction (model 4; Tables 2.6 and 2.7). This model explained about 48% of the variation in year-class survival within the PWS water mass and did not have departures from normality for the error terms. Based on the confidence bands for observed sample values of stability residuals, the regression of year-class survival on condition index was significant and positive at values of stability residuals below -31, not significantly different from zero at values of stability residuals between -31 and -3, and significant and negative at values of stability residuals greater than -3. Therefore, when stability is below average (< -31) just prior to capture within PWS, the relationship between condition index and year-class survival is positive; when stability is above average (>-3) just prior to capture within PWS, the relationship between condition and year-class survival is negative.

Discussion

Stability Hypothesis

Two hypotheses were tested in this study, the *stability hypothesis* and the *survival hypothesis*. For the first part of the *stability hypothesis*, it was postulated that growth rate and fish condition should increase with decreasing stability within PWS, because a slower and weaker development of stratification with a deeper mixed layer depth lengthens phytoplankton production and the interaction between phytoplankton and the springtime zooplankton community, and more organic matter is retained in pelagic food webs. In PWS, the bloom of *Neocalanus*, an important prey item for pink salmon, may be prolonged in the spring due to weak stratification and cooler water temperatures (Willette et al. 1999). Juvenile pink salmon growth and condition could then increase due to the abundance of food resources and the chance of survival could improve with more

alternative prey for their predators (Willette et al. 1999). Contrary to expectation, water column stability just prior to capture did not explain the variability in condition index for either hatchery or wild fish collected from within PWS. PWS stability did explain the growth rate of hatchery fish that originated from within the Sound, although stability explained only a small amount of the variability and did not have the same relationship for each hatchery. While the relationship between stability and growth rate was negative for fish from AFK, SGH and WNH, as hypothesized, the relationship was positive for fish from CCH (Fig. 2.8). Due to the timing of releases, the fish from CCH may differ in their response to the early marine stability conditions in the Sound, juvenile foraging may not be matched to the necessary food resources, or other mechanisms may play a stronger role in explaining the variability in growth rate.

In PWS, large and small calanoid copepods, and harpacticoid copepods were found to be important prey of juvenile pink salmon from April to June. In June, large calanoid copepods and larvaceans became more important in the diet (Cooney et al. 1978; Cooney et al. 1981; Willette 2001). April to June biomass in PWS is dominated by calanoid copepods which peak in June. The smaller calanoid copepods (mainly *Pseudocalanus* spp.) peak in biomass in June, while the large calanoid copepods (mainly *Neocalanus* spp.) peak in May. Upper layer abundance of *Neocalanus* declines rapidly after May as the *Neocalanus* begin to descend to their overwintering depths below 300 m (Fulton 1973; Miller et al. 1984; Cooney et al. 2001). The juveniles from CCH are released into the Sound in late May/early June as their primary food resource, the *Neocalanus* spp., are declining in abundance. Although the copepod *Pseudocalanus* spp. peaks in biomass in June and has a similar energy content per gram to the larger calanoid copepods, it is a much smaller zooplankton. Therefore, a juvenile pink salmon must consume a larger number of *Pseudocalanus* to receive the same energy content in the large copepods as *Neocalanus*.

Stability and year explained less than 5% of the variability in growth rate. Other mechanisms that may play a stronger role in explaining the variability in growth rate

include differences in juvenile pink salmon diets, interannual changes in upper-layer zooplankton stocks, prey-switching behavior, and location of the hatcheries. Juvenile pink salmon diets can vary over small geographic distances (<19km) (Boldt and Haldorson 2003). The quantity of zooplankton forage, especially *Neocalanus* copepods, is not only important in the diet of juvenile salmon, it may also lead to prey-switching behavior in salmon predators such as herring and walleye pollock (Willette et al. 2001). Exchange between the Sound and the waters of the coastal GOA provide oceanic zooplankton subsidies that provide alternate prey for salmon predators and may contribute to increased survival of early marine juveniles, particularly for juveniles originating from hatcheries within the Sound (CCH, SGH, WNH). An increased flow of oceanic zooplankton into PWS in 2002 may have contributed to high survival for this year class of juvenile pink salmon (Kline et al. 2008).

The location of the AFK hatchery compared to the other hatcheries located within the Sound may also play a role in explaining growth rate variability. The Armin F. Koernig hatchery releases its fry very near the open water of the coastal GOA. Fish originating from the three hatcheries further inside the estuary, SGH, WNH, and CCH, must travel about 90 to 140 km to reach the coastal GOA (Willette et al. 2001). Consequently, juveniles from these three hatcheries may reside in the Sound for approximately three to four months (Parker 1997), while fry released from the AFK hatchery immediately migrate to the GOA-adjacent waters of Elrington Passage where they may stay for up to two months before outmigrating to the open ocean (Urquhart 1979). Therefore, the local environment of the estuary would be expected to have a greater influence on the growth and condition of fry from the estuarine hatcheries, while fry from AFK are more likely to be influenced by the Alaska Coastal Current.

For the second part of the *stability hypothesis*, it was postulated that fish condition increases with increasing stability within the northern coastal GOA. With sufficient light levels, greater water column stability, and shallowing of the mixed layer depth, an increase in primary production during the spring bloom should lead to elevated secondary

production and higher marine survival rates of salmon in the GOA. Contrary to expectation, stability effects were not statistically significant in explaining variability in condition index within either the ACC or shelf water masses (Figs 2.10 and 2.11).

Although it was postulated that a shallower mixed layer depth in the spring is important for juvenile pink salmon survival in the GOA, this hypothesis was not directly tested since mixed layer depth and stability are related. The mixed layer depth, in this study, is defined as the bottom of the quasi-homogenous region in the upper ocean where there is little change in density with depth. It is determined by a balance between destabilizing effects of wind forcing, surface cooling, evaporation, and turbulent mixing and stabilizing effects of surface heating and freshwater influx (Sarkar et al. 2005). Turbulent mixing can easily overturn a mixed layer. The larger the density difference across the bottom of the mixed layer and the larger the density gradient in the lower layer, the more stable the water column because turbulent mixing is suppressed and more energy is needed to mix the water column (Kara et al. 2003). Hence, the more stable the water column, the shallower the mixed layer depth. Interannual and seasonal changes in the mixed layer depth cause variations in the resupply of nutrients to the euphotic zone and overall production of phytoplankton. When salmonids are present to consume the zooplankton, the optimal mixed layer depth for young salmonid survival is a depth that promotes an in-phase cycle between phytoplankton and zooplankton production (Parsons and Kessler 1987).

Although the *stability hypothesis* was based on the ocean conditions in the spring to early fall, the seasonal cycle of changes in stratification and mixed layer depth that lead up to the spring bloom are just as important. During the winter in the GOA, the mixed layer is deepest due to high wind stress that causes vertical mixing and coastal convergence and the water column is less stratified due to minimum freshwater discharge, cool temperatures, high wind stress, and increased evaporation (Sarkar et al. 2005). This part of the seasonal cycle is important for nutrient entrainment from depth and replenishment of nutrients to the surface waters. During the spring, winds decrease

and solar radiation increases, shoaling the mixed layer and increasing the surface stability. The phytoplankton concentrations 'bloom' from the increases in available light and may concentrate zooplankton in the surface waters, reducing foraging costs for pink salmon (Aydin et al. 2005). With the eventual depletion of nutrients within the euphotic zone, phytoplankton production will be limited and seasonal deepening of the mixed layer is necessary for replenishment of nutrients to the surface (Freeland et al. 1997). In the early fall, an increase in winds again deepen the mixed layer.

Large interannual differences in the timing of stratification onset and complex stratification processes in the northern GOA make applying the *stability hypothesis* more complicated than in regions where vertical heat fluxes drive stability (Weingartner 2007). Other studies have found that stratification is *not* required for a spring bloom to occur in regions such as the Gulf of Maine and the Norwegian Sea (Townsend et al. 1992; Ellertsen 1993; Dale et al. 1999), but instead the cessation of the mixed layer deepening is more important (Evans and Parslow 1985). Therefore, another mechanism besides water column stability may better explain annual variations in pink salmon growth and condition.

Survival Hypothesis

For the *survival hypothesis,* it was postulated that there is an interactive effect between fish condition and environmental factors, such as water column stability, on the variability in year-class survival. While stability just prior to capture and condition index were both important in explaining the variability in year-class survival within PWS, condition index was important within the ACC water mass, and neither condition index nor stability were statistically significant within the shelf water mass.

Body condition, a measure of an animal's physiological state, is potentially related to its evolutionary fitness (Jakob et al. 1996). Fish that migrate to the marine environment at a larger body size tend to have a higher survival rate when compared to their smaller counterparts (Quinn 2005). In this study, cohorts with individuals heavier at a given

length sampled during the year of release within the ACC water mass experienced higher survival during the return year, the following spring, but there was no clear relationship between fish condition and survival within the shelf water mass. An individual's condition in one life stage may not directly relate to a survival advantage until a later life stage. For example, among and within Snake River Chinook salmon (*O. tshawytscha*) populations, fish condition during the summer in their freshwater rearing habitats was not strongly related to survival at downstream sites the following spring (Zabel and Achord 2004).

The relationship between condition index and year-class survival was positive when stability was below average just prior to capture within PWS; the relationship between condition and year-class survival was negative when stability was above average just prior to capture within PWS. This follows with earlier studies that concluded that slower and weaker development of stratification with a deeper mixed layer depth may be more important for juvenile pink salmon survival in PWS (Eslinger et al. 2001).

There were some limitations in this study. Although some of the relationships between stability, condition index, growth rate, and survival were statistically significant, the significance may be overstated because of sample pseudoreplication. The marine survival rates of juvenile hatchery pink salmon that originate from within PWS (CCH, SGH, WNH) are correlated (Pyper et al. 2001). These juveniles are subject to the influence of the same biological and physical processes (temperature, food resources, competition, predation) at local and regional scales and have similar migratory habits (Farley and Munk 1997; Pyper et al. 2001). Therefore, within a single year, the fish originating from the three hatcheries located within PWS and the wild fish may not be statistically independent samples.

Although this study only found one strong relationship between water column stability, condition, and marine survival of salmon, there is indirect support for the 'optimal stability window' hypothesis in northern regions. In PWS, mortality of pink salmon was negatively correlated with the duration of the copepod bloom during the

juvenile life stage in PWS (Willette et al. 1999) and in the coastal GOA, increased water column stability was linked to increased chlorophyll-*a* concentrations, longer bloom duration, and earlier onset of the spring bloom (Henson 2007), supporting a link between primary production and water column stability. Based on stability and zooplankton measurements in the Bering Sea, an optimal stability 'window' was hypothesized to exist on the eastern Bering Sea shelf. As stability increases past the 'optimal' level, post-bloom production on the middle shelf declines, large grazers cannot be supported, and there is a reorganization of the trophic levels present on the southeastern Bering Sea middle shelf. Relative to 1999, in 2004 the shelf zooplankton community shifted from large to small species, water column stability increased three-fold, and young-of-year walleye pollock diets shifted from large to small copepods (Coyle et al. 2008).

In conclusion, stability is only one possible mechanism linking oceanographic conditions and marine survival of salmon (Gargett 1997). Further understanding of the how oceanographic processes affect the biology of the marine phase of salmon will lead to better predictions of hatchery and wild salmon returns and a better grasp at how climate changes will affect the marine survival of Pacific salmon.

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Tables

Table 2.1 Subsets of the fish data including dates the fish were sampled, the number of hauls sampled, and the transects where the fish were sampled, by water mass (Prince William Sound, Alaska Coastal Current water mass, shelf water mass). Sample dates are listed as year and month/day. ACC: Alaska Coastal Current; CC: Cape Cleare; CF: Cape Fairfield; GP: Gore Point; PWS: Prince William Sound; SL: Seward Line

Fish variable*	Sample dates†	Number of hauls	Transect	Water mass
Growth rate	1998 (6/24-6/26)	12	PWS	PWS
	1999 (6/21-7/5)	51	PWS	PWS
	2000 (6/23-7/8)	27	PWS	PWS
	2001 (6/19-8/16)	59	PWS	PWS
	2002 (6/18-7/22)	26	PWS	PWS
	2003 (6/17-8/4)	40	PWS	PWS
	2004 (6/17-7/22)	26	PWS	PWS
Condition index	1998 (7/16-7/18)	11	PWS	PWS
	2001 (7/7-9/20)	50	PWS	PWS
	2002 (7/21-8/20)	11	PWS	PWS
	2003 (7/16-8/4)	12	PWS	PWS
	2004 (7/21-7/22)	12	PWS	PWS
Condition index	1998 (8/2-10/9)	6	GP, SL	ACC
	1999 (8/27)	4	SL	ACC
	2000 (8/12-8/14)	7	GP, SL	ACC
	2001 (7/8-9/18)	25	CC, SL	ACC
	2002 (7/20-8/23)	12	SL	ACC
	2003 (7/13-9/15)	49	CC, CF, GP, SL	ACC
	2004 (7/20-9/12)	15	CF, SL	ACC
Condition index	1997 (7/27)	9	GP	shelf
	1998 (8/1-10/8)	6	SL	shelf
	1999 (8/28-10/9)	4	SL	shelf
	2000 (8/12-8/20)	37	GP, SL	shelf
	2001 (7/9-9/19)	43	GP, SL	shelf
	2002 (7/22-8/23)	42	CC, GP, SL	shelf
	2003 (7/25-9/11)	40	CC, CF, GP, SL	shelf
	2004 (7/20-7/24)	10	CF, SL	shelf

*The collections originated from four projects; 1. The Alaska Department of Fish and Game PWS monitoring program (1998-2004), 2. the NOAA National Marine Fisheries Service Ocean Carrying Capacity Program (1997-1998, 2000-2003), Jamal Moss and Ed Farley, 3. University of Alaska Fairbanks (UAF) United States Global Ocean Ecosystem Dynamics Northeast Pacific program (U.S. GLOBEC NEP) (1998-2004), and 4. the UAF Alaska Predator Ecosystem Experiment (APEX) project (1998), Jennifer Boldt.

†Not every date was sampled within a given range.

Table 2.2 Year of release (sampling year), hatchery, release group, release dates in May (unless specified), release weights in grams, and survival by hatchery of origin for the four hatcheries. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

Release year	Hatchery	Release group*	Release date (May)	Release weight (g)	Return year survival (%)†
1998	AFK	AFK	7	0.45	8.7
1999	AFK	AFK	April 30	0.29	5.2
2000	AFK	AFK, AFK00	4, 24	0.39, 0.47	3.4
2001	AFK	AFK, AFK01	7, 23	0.46, 0.48	5.2
2002	AFK	AFK	10	0.43	4.5
2003	AFK	AFK, AFK03, AFK03_3	1, 12, 19	0.68, 0.97, 1.0	3.6
2004	AFK	AFK, AFK04, AFK04_3	6, 20, 20	0.54, 0.66, 0.72	6.1
1999	CCH	CCH	24	0.30	5.0
2000	CCH	CCH	June 8	0.34	1.6
2001	CCH	CCH	31	0.32	1.1
2003	CCH	CCH	31	0.68	2.0
2004	CCH	CCH	20	0.37	9.6
2000	SGH	SGH	12	0.50	8.1
2001	SGH	SGH	18	0.60	2.5
1998	WNH	WNH	1	0.49	9.1
1999	WNH	WNH, WNH99	20, April 29	0.66, 0.50	7.1
2000	WNH	WNH, WNH00	16, 19	0.40, 0.50	6.2
2001	WNH	WNH, WNH01	7, 17	0.71, (0.69-0.70)	4.4
2002	WNH	WNH, WNH02	10, 19	0.60, 0.69	16.8
2003	WNH	WNH, WNH03, WNH03_3	1, 7, 14	0.74, 0.85, 1.09	2.3
2004	WNH	WNH, WNH04, WNH04_3	7, 20, 20	0.58, 0.59, 0.73	6.5

*Each combination of a hatchery release date and release weight is considered a release group. Hatcheries may have had more release groups, but only the sampled release groups are listed.

†Smolt to adult survival, in percent.

Table 2.3 Comparison of models for the fish variable standardized growth rate. The term 'origin' represents the four hatchery groups. The abbreviation 'p' stands for number of estimated parameters, RSS is the residual sum of squares, and 'adj R^2' is the adjusted R squared.

		Prince William Sound *			
Model	Terms	*p*	RSS	ΔAICc	adj R^2
1	$Stab^2$, Origin, $Stab^2$ x Origin	12	944.2	4.6	0.04
2	$Stab^2$, Origin	7	990.8	5.3	0.01
3	$Stab^2$	4	1004.7	2.3	0.01
4	Stab, Origin, Stab x Origin	9	952.1	**0.0**	0.04
5	Stab, Origin	6	996.7	4.6	0.01
6	Stab	3	1013.9	2.5	0.01
7	Origin	5	999.6	3.2	0.01
8	Year, Origin, Year x Origin	22	849.8	2.5	0.09
9	Year, Origin	11	944.2	2.4	0.04
10	Year	8	963.0	**0.6**	0.03
11	null model	2	1023.5	2.7	NA

*n=241

Table 2.4 Summary of the best fit model for the fish variable standardized growth rate.

	Coefficient	Standard Error
Model 4:		
Dependent variable: **Standardized growth rate**	R^2_{adj}=0.0418, F=2.494 on 7 and 233 d.f., P=0.0173	
Prince William Sound		
Intercept	-0.3697	0.2449
Stab	-0.0006	0.0198
CCH	0.4403	0.4274
SGH	5.1215	2.5501
WNH	0.2209	0.3450
Stab x CCH	0.0481	0.0350
Stab x SGH	-1.0214	0.4539
Stab x WNH	-0.0301	0.0253

Table 2.5 Comparison of models for the fish variable condition index. The term 'origin' represents the four hatchery groups along with the wild group. The abbreviation 'p' stands for number of estimated parameters, RSS is the residual sum of squares, and 'adj R^2' is the adjusted R squared.

		Prince William Sound *				*Gulf of Alaska (ACC)* †				*Gulf of Alaska (shelf)* ‡			
Model	Terms	*p*	RSS	ΔAICc	adj R^2	*p*	RSS	ΔAICc	adj R^2	*p*	RSS	ΔAICc	adj R^2
1	$Stab^2$, Origin, $Stab^2$ x Origin	16	0.0303	20.4	0.01	16	0.0610	33.3	0.13	16	0.1127	60.2	0.04
2	$Stab^2$, Origin	8	0.0326	6.4	0.01	8	0.0710	31.0	0.06	8	0.1236	59.5	<0.01
3	$Stab^2$	4	0.0336	0.0	0.03	4	0.0784	33.8	<0.01	4	0.1263	55.0	<0.01
4	Stab, Origin, Stab x Origin	11	0.0334	16.1	0.05	11	0.0674	32.0	0.08	11	0.1212	62.4	<0.01
5	Stab, Origin	7	0.0338	7.4	0.01	7	0.0710	28.7	0.07	7	0.1250	59.4	0.01
6	Stab	3	0.0350	1.8	<0.01	3	0.0784	31.7	0.01	3	0.1274	54.6	0.01
7	Origin	6	0.0342	6.1	0.01	6	0.0715	27.4	0.07	6	0.1250	57.3	<0.01
8	Year, Origin, Year x Origin	24	0.0305	47.2	0.13	28	0.0397	19.4	0.36	33	0.0794	38.5	0.26
9	Year, Origin	10	0.0327	11.5	0.01	12	0.0503	0.0	0.31	13	0.0876	5.0	0.27
10	Year	6	0.0341	6.0	0.01	8	0.0574	5.9	0.24	9	0.0895	0.0	0.27
11	null model	2	0.0353	0.3	NA	2	0.0795	31.2	NA	2	0.1274	52.6	NA

*n=96, †n=118, ‡n=191

Table 2.6 Comparison of models for year-class survival. The abbreviation 'p' stands for number of estimated parameters, RSS is the residual sum of squares, and 'adj R^2' is the adjusted R squared.

			Prince William Sound *			*Gulf of Alaska (ACC)* †			*Gulf of Alaska (shelf)* ‡		
Model	Terms	*p*	RSS	ΔAICc	adj R^2	RSS	ΔAICc	adj R^2	RSS	ΔAICc	adj R^2
1	$Stab^2$, $Condition^2$, $Stab^2$ x $Condition^2$	10	0.0010	24.8	0.79	0.0072	22.8	0.44	0.0189	19.0	0.12
2	$Stab^2$, Condition, $Stab^2$ x Condition	7	0.0032	8.2	0.51	0.0132	13.7	0.20	0.0252	9.9	0.03
3	Stab, $Condition^2$, Stab x $Condition^2$	7	0.0037	10.4	0.43	0.0094	6.9	0.43	0.0266	11.3	0.03
4	Stab, Condition, Stab x Condition	5	0.0041	**0.0**	0.48	0.0138	5.6	0.26	0.0298	6.3	0.04
5	$Stab^2$, $Condition^2$	6	0.0046	7.4	0.36	0.0139	9.9	0.21	0.0279	8.3	0.02
6	$Stab^2$, Condition	5	0.0065	7.4	0.17	0.0143	6.2	0.24	0.0296	6.1	0.03
7	Stab, $Condition^2$	5	0.0086	12.0	0.10	0.0140	5.8	0.26	0.0284	5.1	0.01
8	Stab, Condition	4	0.0086	7.6	0.01	0.0143	2.7	0.28	0.0298	3.1	0.01
9	$Stab^2$	4	0.0065	3.1	0.24	0.0214	10.7	0.07	0.0320	4.8	0.06
10	$Condition^2$	4	0.0097	9.6	0.15	0.0142	2.5	0.29	0.0303	3.5	0.01
11	Stab	3	0.0086	4.0	0.06	0.0214	7.5	0.01	0.0320	**1.9**	0.01
12	Condition	3	0.0097	5.9	0.07	0.0147	**0.0**	0.31	0.0315	**1.5**	<0.01
13	null model	2	0.0098	3.0	NA	0.0223	5.6	NA	0.0330	**0.0**	NA

*n=16, †n=20, ‡n=24

Table 2.7 Summary of the best fit models using year-class survival from hatchery fish as the dependent variable and condition index and stability as the continuous independent variables.

	Coefficient	Standard error
Model 4:		
Dependent variable: **Year-class survival**	R^2_{adj}=0.4799 F=5.614 on 3 and 12 d.f., P=0.0122	
Prince William Sound		
Intercept	0.0643	0.0096
Stab	0.0012	0.0005
Condition	-2.0111	0.8058
Stab x Condition	-0.1235	0.0338
Model 12:		
Dependent variable: **Year-class survival**	R^2_{adj}=0.3058, F=9.37 on 1 and 18 d.f., P=0.0067	
Gulf of Alaska (ACC)		
Intercept	0.0713	0.0076
Condition	0.7840	0.2561

Figures

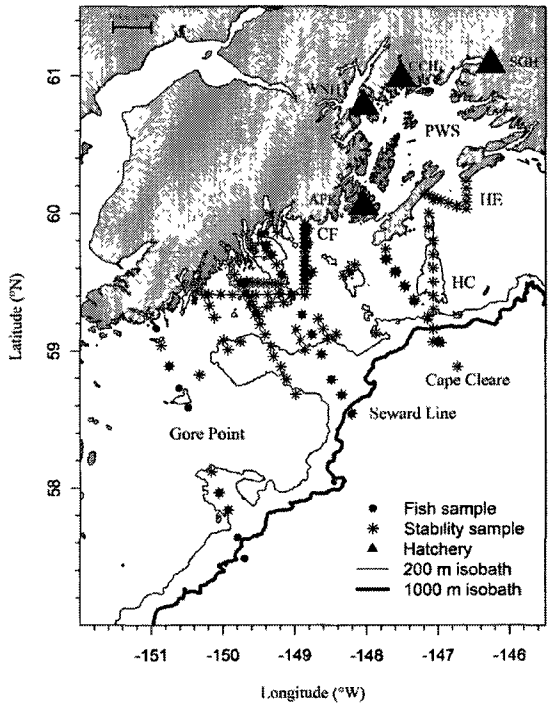

Figure 2.1 Locations where fish samples (filled circles) and stability* samples (stars) were collected within the northern coastal Gulf of Alaska. The hatcheries of origin are represented by the filled triangle symbol. Isobaths are shown at 200 m and 1000 m. The main transects are labeled. CF: Cape Fairfield; HC: Hinchinbrook Canyon; HE: Hinchinbrook Entrance; Hatcheries are also labeled. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

*Stability collections originated from four projects: 1. Jamal Moss and Ed Farley, National Marine Fisheries Service, NOAA, Ocean Carrying Capacity Program (1997-1998, 2000-2003), 2. Russell Hopcroft and Tom Weingartner, University of Alaska Fairbanks (UAF) Institute of Marine Science, Long Term Observation Program (LTOP) (1997-2004), 3. UAF U.S. Global Ocean Ecosystem Dynamics Northeast Pacific Program (2001-2004), and 4. Suzanne Strom, Western Washington University, and Tom Weingartner, UAF Institute of Marine Science, process-oriented projects (PROCESS) conducted by researchers from NOAA and several universities (2001, 2003). The LTOP and PROCESS cruise data can be accessed at: http://globec.whoi.edu/jg/dir/globec/.

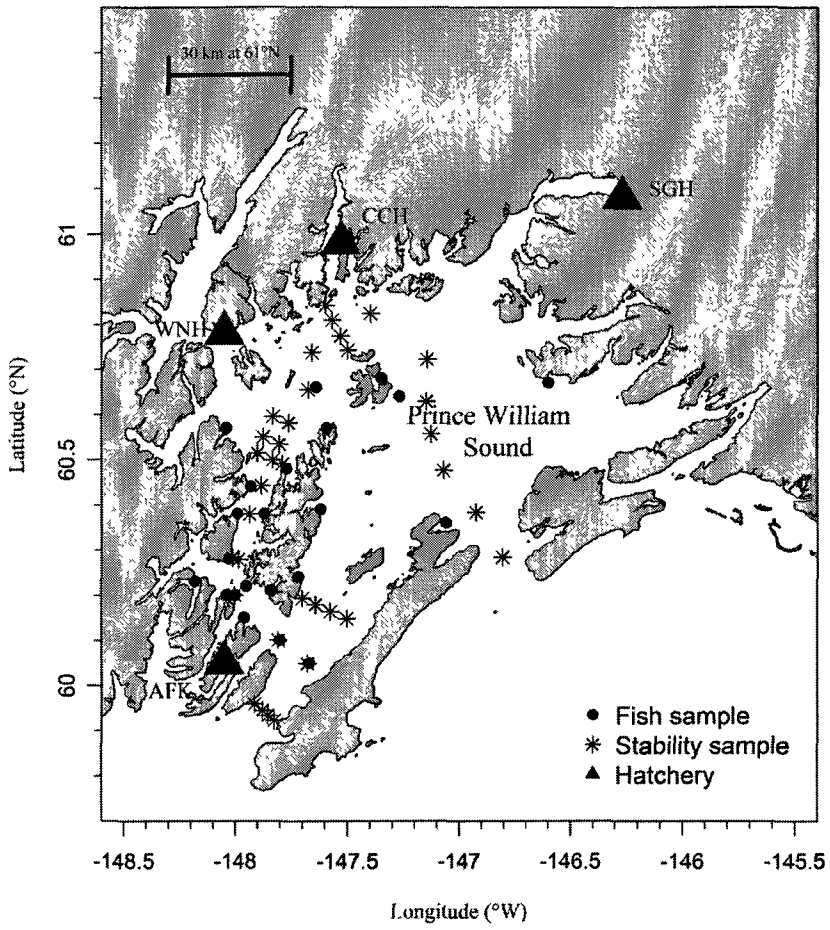

Figure 2.2 Locations where fish samples (filled circles) and stability samples (stars) were collected within Prince William Sound. The hatcheries of origin are represented by the filled triangle symbol. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

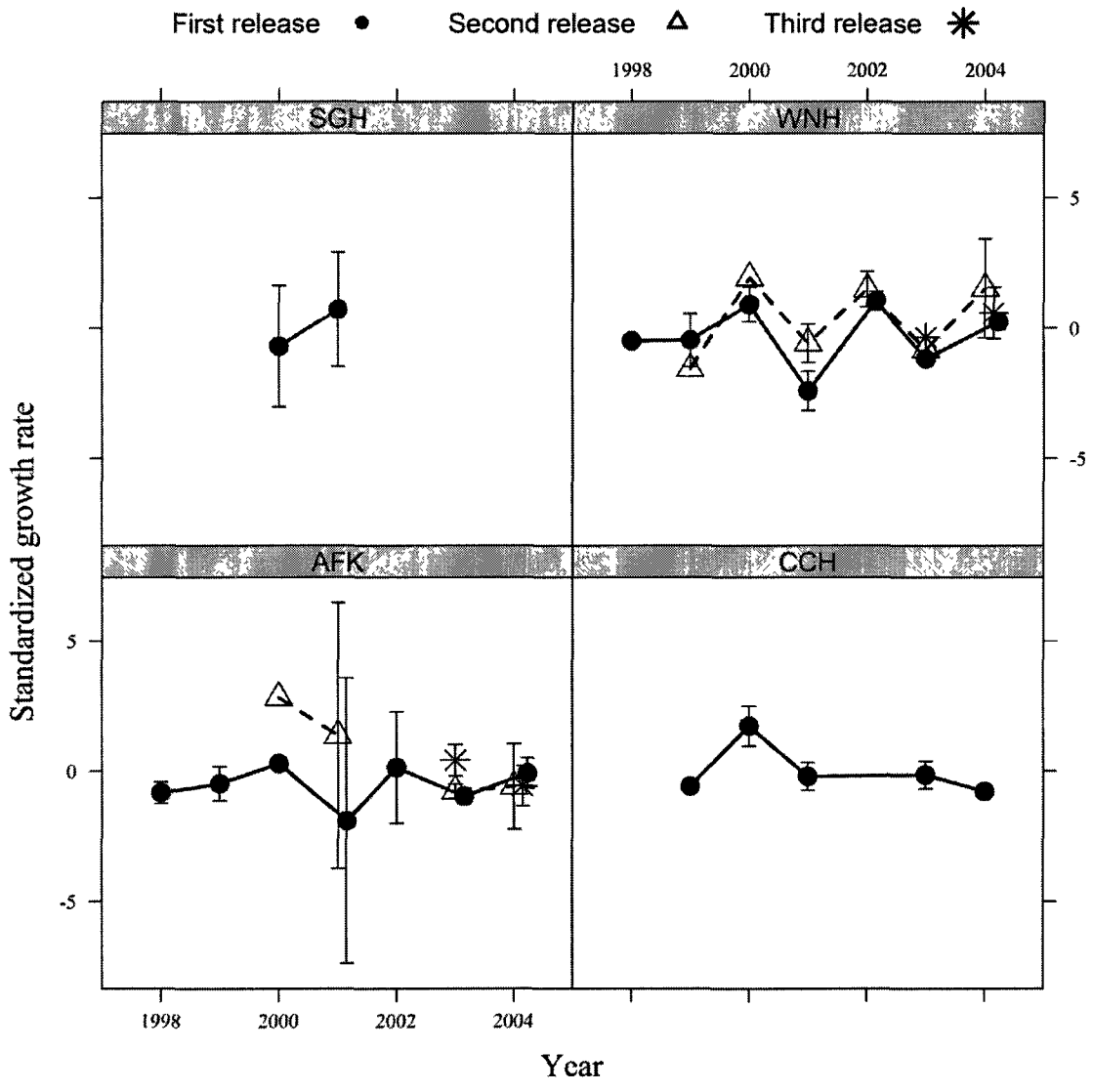

Figure 2.3 Standardized growth rate for fish of hatchery origin from sampling years 1998 through 2004. The fish samples were collected within Prince William Sound. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

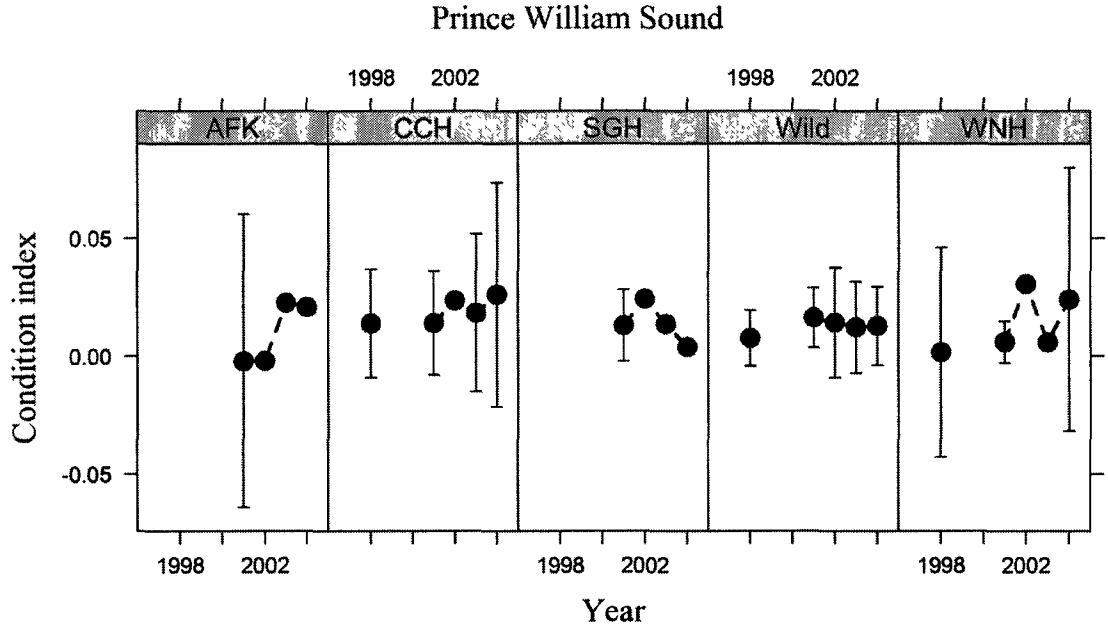

Figure 2.4 Condition index for fish of hatchery and wild origin from sampling years 1998 through 2004. The fish samples were collected within Prince William Sound. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

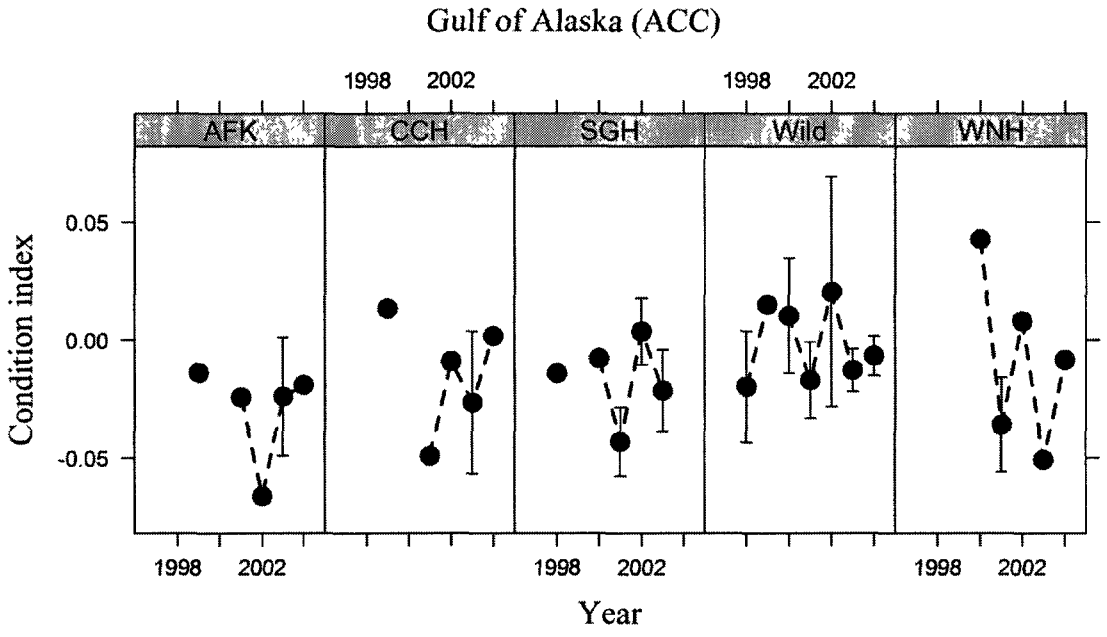

Figure 2.5 Condition index for fish of hatchery and wild origin from sampling years 1998 through 2004 collected within the Alaska Coastal Current (ACC) water mass. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

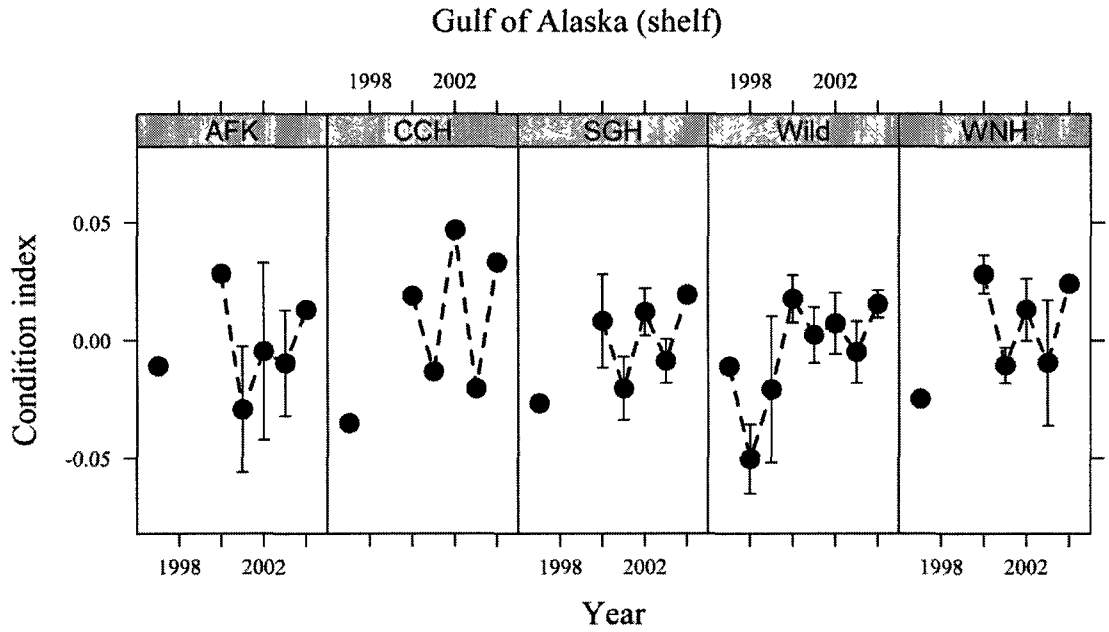

Figure 2.6 Condition index for fish of hatchery and wild origin from sampling years 1997 through 2004 collected within the shelf water mass. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

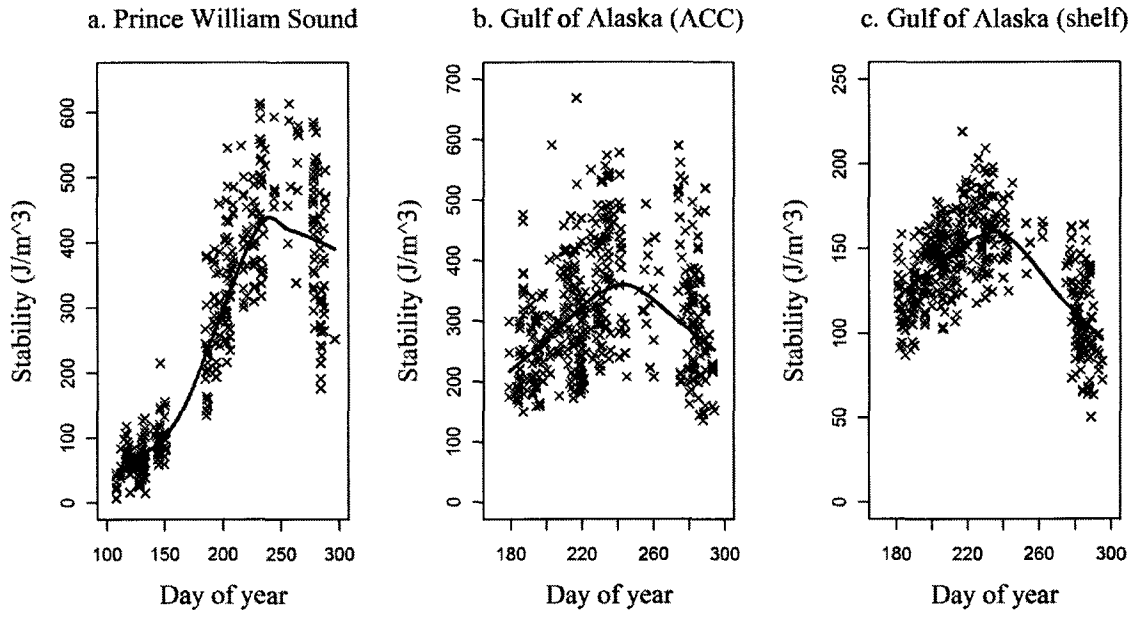

Figure 2.7 Stability by day of year for each water mass (Prince William Sound (PWS), Alaska Coastal Current (ACC), shelf) used to calculate average stability residuals from within two weeks before and after the hatchery release date, or from within two weeks prior to the fish capture date. A smoothing parameter of 0.45 was used for PWS, 0.70 for the ACC water mass, and 0.75 for the shelf water mass.

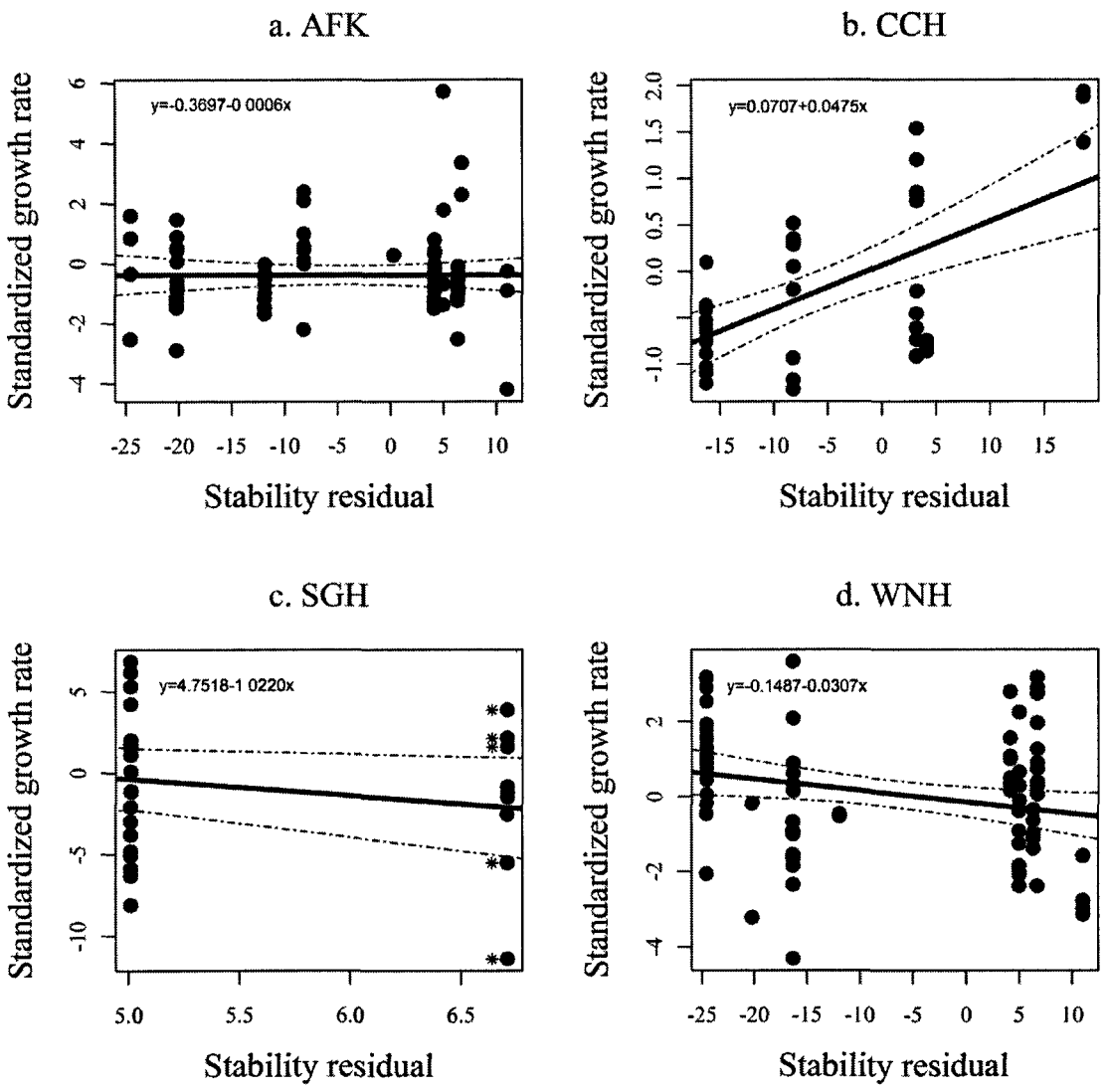

Figure 2.8 Relationship between standardized growth rate by haul and stability residual measurements (with 95% confidence bands) collected from within Prince William Sound. Plot 'a' highlights the Armin F. Koernig hatchery (AFK) data, plot 'b' highlights the Cannery Creek hatchery (CCH) data, plot 'c' highlights the Solomon Gulch hatchery (SGH) data, and plot 'd' highlights the Wally Noerenberg hatchery (WNH) data. The six influential outliers from hauls of SGH fish are labeled with stars.

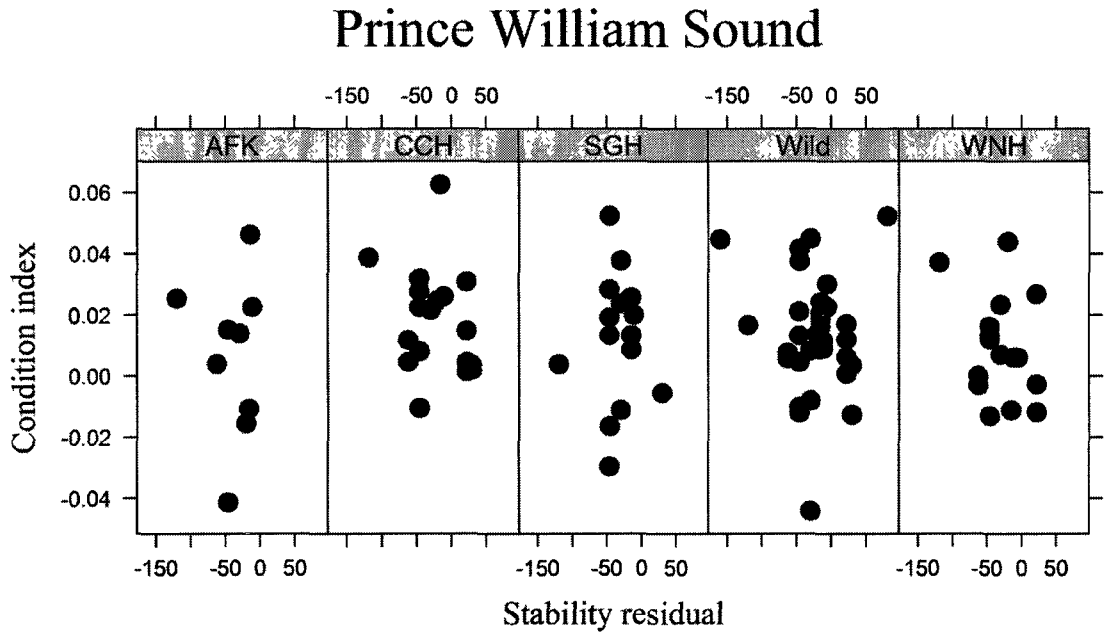

Figure 2.9 Relationship between fish condition index by haul and stability residual measurements collected from within Prince William Sound. Each plot is a different origin. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

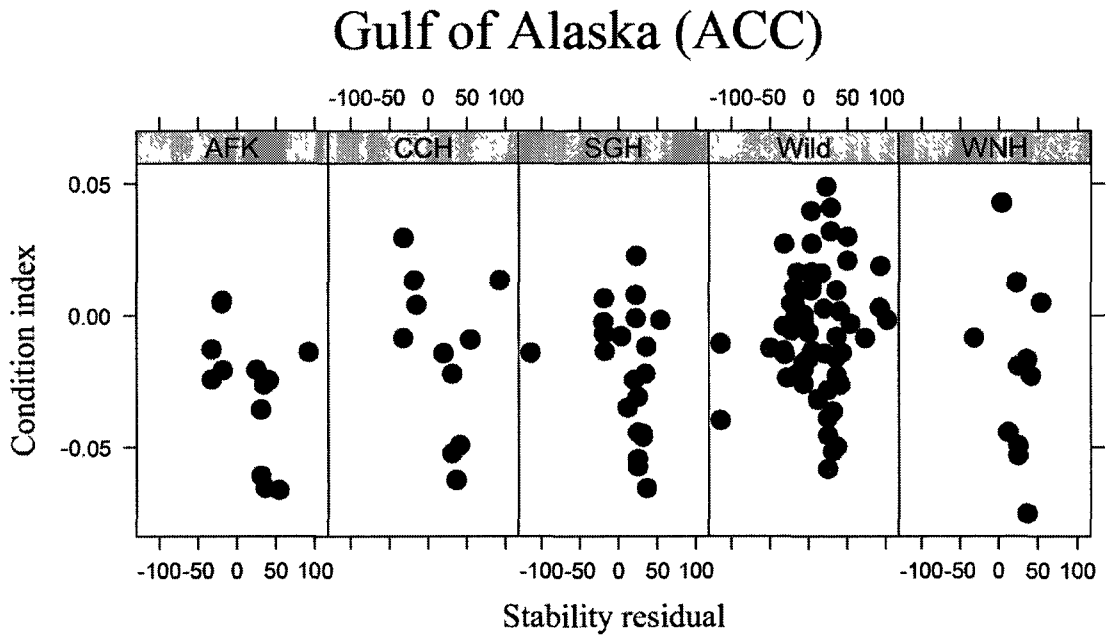

Figure 2.10 Relationship between fish condition index by haul and stability residual measurements collected from within the Alaska Coastal Current (ACC) water mass. Each plot is a different origin. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

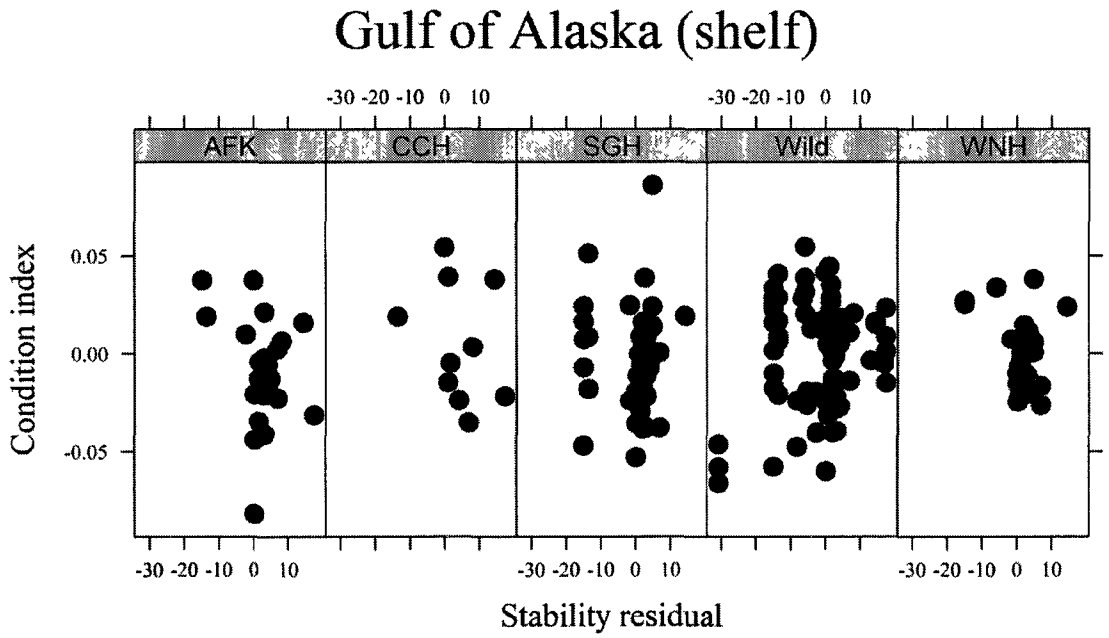

Figure 2.11 Relationship between fish condition index by haul and stability residual measurements collected from within the shelf water mass. Each plot is a different origin. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

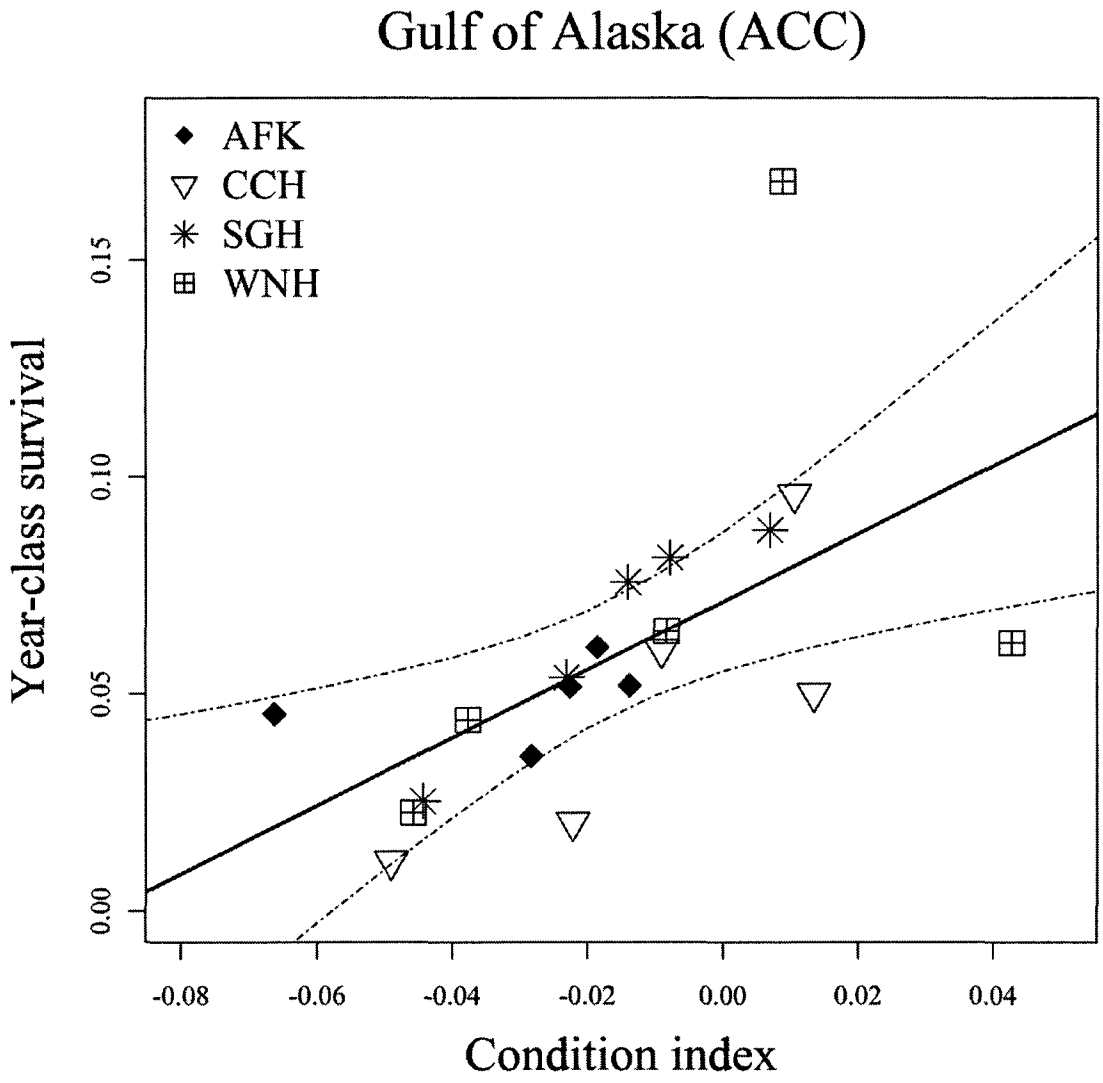

Figure 2.12 Relationship between year-class survival and fish condition index within the Alaska Coastal Current (ACC) water mass. Ninety five percent confidence intervals are shown as dotted lines. AFK: Armin F. Koernig hatchery; CCH: Cannery Creek hatchery; SGH: Solomon Gulch hatchery; WNH: Wally Noerenberg hatchery

Chapter 3: Differences in stability effects on the marine survival of hatchery pink salmon (*Oncorhynchus gorbuscha*) within the upwelling and downwelling domains of the northeast Pacific Ocean[1]

ABSTRACT

Regional coastal conditions have a strong influence on juvenile salmon survival during their critical first months in the marine environment. Salmon (genus *Oncorhynchus)* survival has been thought to be favored within the high latitude downwelling domain if water column stabilities increase, whereas stability may have the opposite effect in upwelling-dominated lower latitudes. In this study, the relationships between water column stabilities during early marine residence of pink salmon (*O. gorbuscha*) in both the upwelling and downwelling domains of the northeast Pacific Ocean and marine survival rates for hatchery stocks ranging from Vancouver Island, British Columbia, to Kodiak Island, Alaska, were explored. Contrary to expectation, there was no clear difference in the effect of stability on marine survival rates in the downwelling and upwelling domains. In both domains, marine survival rates increased for pink salmon stocks that experienced below-average stability on the inner shelf during early marine residence. Stability effects from the outer shelf showed no consistent relationship to marine survival within the northeast Pacific.

Key Words: Gulf of Alaska, British Columbia, *Oncorhynchus gorbuscha,* pink salmon, stability effects, marine survival, potential energy anomaly, west coast of Vancouver Island, upwelling domain, downwelling domain

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[1]Miller, S.E., M.D. Adkison, and L. Haldorson. 2011. Differences in stability effects on the marine survival of hatchery pink salmon (*Oncorhynchus gorbuscha*) within the upwelling and downwelling domains of the northeast Pacific Ocean. Prepared for submission to Fisheries Oceanography.

INTRODUCTION

Salmon (genus *Oncorhynchus*) survival is strongly influenced by processes affecting them during their first year in the coastal ocean (Francis and Hare, 1994) and coastal conditions at scales less than 500 km have a greater influence on survival rate and recruitment than large-scale climate patterns (Pyper *et al.,* 2001; Mueter *et al.,* 2002a; Mueter *et al.*, 2002b). Stability-induced changes in the availability of light and nutrients for the production of phytoplankton are reflected in secondary production and could then ultimately affect the marine survival rates of juvenile salmon in the eastern North Pacific. By restricting turbulence, an increase in stability allows more phytoplankton to remain in the euphotic zone, but it also leads to a decrease in the resupply of nutrients to the surface. A weakly stratified water column allows a resupply of nutrients to surface waters, but may move phytoplankton over larger vertical distances and out of the euphotic zone (Gargett, 1997). There is a 'window' at intermediate levels of light and nutrients where phytoplankton production is at its maximum. The high latitude downwelling domain, where macronutrients are plentiful but primary production is limited through low light levels during part of the year, occupies the low-stability end of the optimal 'window.' The low latitude upwelling domain, where light levels are higher and more uniform throughout the year but macronutrients are limited in the surface layer, occupies the high-stability end of the optimal 'window.' Salmon survival is hypothesized to be favored within the downwelling domain if water column stabilities increase, whereas stability may have the opposite affect at lower latitudes (Gargett, 1997).

In this study, relationships between regional water column stabilities during early marine residence and marine survival rates of hatchery pink salmon (*O. gorbuscha*) stocks were explored. The hatchery stocks ranged from Vancouver Island, British Columbia, to Kodiak Island, Alaska.

Juvenile pink salmon originating from southeastern, south-central, and western Alaska enter the coastal Gulf of Alaska (GOA), and travel west/northwest as they follow the Alaska Coastal Current (ACC), while juvenile pink salmon originating from British

Columbia and Washington travel north and west along the coast (Takagi *et al.,* 1981). These juveniles distribute themselves across the entire continental shelf in surface waters, but are rarely found past the shelf break (Welch *et al.*, 2003). During the summer, in the first few months in these coastal areas, they experience the coastal upwelling domain (Baja California to Vancouver Island) or the coastal downwelling domain (Queen Charlotte Sound to the Aleutian Islands) of the northeast Pacific Ocean.

From late March to September, the waters off Vancouver Island are considered part of the upwelling domain (Thomson, 1981). On the shelf of the west coast of Vancouver Island (WCVI), a persistent and low surface salinity current, the Vancouver Island Coastal Current, flows northward within about 25 km of the coast (Thomson *et al.,* 1989), while a wind-driven current flows southward along the shelf break (Freeland *et al.,* 1984). The shelf and shelf break/slope regions off the WCVI differ in total zooplankton biomass, species composition, nutrients, and phytoplankton distributions. The inner shelf has higher average surface layer nitrate and chlorophyll concentrations, and an earlier and narrower zooplankton biomass peak (May-June), while the shelf break/slope region has a longer total zooplankton biomass peak that occurs in the summer (Mackas, 1992).

The region from southeast Alaska to Kodiak Island, Alaska is representative of the downwelling domain. This coastal domain can be divided into two water masses, the inner and outer shelf water masses. The inner shelf water mass lies less than 50 km from the coast in the summertime and is mainly influenced by the low-salinity, nutrient poor ACC. The migration band of juvenile pink salmon is influenced by the strength and location of the ACC, which can affect salmon production; a significant portion of the early growth for juvenile pink salmon occurs in the ACC over the continental shelf from July to October (Cooney, 1984). The outer shelf water mass lies from about 50 to 150 km from the coast in the summertime and is influenced by the more saline and nutrient rich Alaskan Stream. While salinity controls the outer shelf stratification in the fall through winter, temperature is the main control of stratification in the spring and summer. Except

in late winter, stratification over the outer shelf is always weaker than over the inner shelf water mass (Weingartner, 2007).

Salmon abundance and survival rates in the upwelling and downwelling domains of the northeast Pacific Ocean are often asynchronous (Francis and Sibley, 1991; Hare *et al.,* 1999; Hobday and Boehlert, 2001; Mueter *et al.,* 2002a) and the upwelling and downwelling domains occupy opposite ends of the optimal stability 'window' (Gargett, 1997). Therefore, it was hypothesized that in the coastal downwelling domain salmon survival should improve when water column stability within coastal regions increases during the summer of early marine residence. Water column stability should have the opposite effect on marine survival within the upwelling domain.

METHODS

Marine Survival Data

Survival, y, was calculated as the ratio of returning adults (returns to the hatchery plus harvest estimates) to fry released one year earlier using estimates obtained from each hatchery of origin (Figs 3.1 and 3.2, Table 3.1). Sixteen hatcheries (twenty-two stocks) of hatchery pink salmon were included in the dataset. The survival data series ranged from one to 14 brood years per stock (brood years 1976 to 2007). Four hatcheries within Prince William Sound were treated as separate stocks before and after brood year 1995 since coded wire tagging was replaced by thermal otolith marking in brood year 1995 and to ensure comparability of survival rates. Puntledge River Hatchery and Quinsam River Hatchery were separated into fed and unfed fry stocks, since separate survival rates were available for each.

Based on visual inspection and the Shapiro-Wilks normality test, the survival data was positively skewed and not normally distributed. Therefore, to normalize the data, the square root of the survival ratio was arcsine-transformed.

Potential Energy Anomaly (Stability)

Hydrographic samples were collected from stations off Kodiak Island, Alaska, to stations off the west coast of Vancouver Island from the end of June to the end of August (day of year 175 to 244) from 1976 through 2008 (Figs 3.3 and 3.4, Table 3.2). The upper water column stability (ϕ) was estimated for each sample using the potential energy equation,

$$\phi = \frac{1}{h}\int_{-h}^{0}(\bar{\sigma}_\theta - \sigma_\theta)gzdz;\ \bar{\sigma}_\theta = \frac{1}{h}\int_{-h}^{0}\sigma_\theta dz\ \left(\mathrm{Jm^{-3}}\right);\ \sigma_\theta = \rho_{S,\theta,0} - 1000\ \mathrm{kg\ m^{-3}}, \quad (3.1)$$

Simpson *et al.,* (1977). The potential energy equation calculates the work required to bring about the vertical redistribution of the mass during complete mixing. A strongly stratified (more stable) water column requires more energy to mix than a weakly stratified water column. In equation 3.1, h is the water column depth, z is the vertical coordinate, g is the acceleration of gravity (9.81 m s^{-2}), and ρ is the density of sea water by depth (kg m^{-3}) calculated using salinity (S), potential temperature (θ), and atmospheric pressure (Stewart, 2007). The variable σ_θ is the density of a water parcel when it has been removed adiabatically to the reference pressure 0 dbar. Units for the potential energy anomaly equation are in Joules per cubic meter. One meter depth intervals over a depth range from 1 to 100 were used in the calculation. Stability was calculated separately for each hydrographic profile. Stability was computed for a total of n=2,034 individual hydrographic profiles.

With the exception of the long-term time series at oceanographic station GAK 1 on the Seward Line transect and the data collected by NOAA's Pacific Marine Environmental Laboratory (PMEL) group in 2001, any hydrographic profile missing more than ten sequential intervals was excluded. To increase the amount of available data, data from the long-term time series at oceanographic station GAK 1 (59° 50.7' N, 149° 28.0' W) (http://www.ims.uaf.edu/gak1/, accessed: July 1, 2010) (Royer, 1982; Weingartner *et al.*, 2005) (Table 3.2) was included in the hydrographic samples for the

inner shelf water mass. Oceanographic station GAK 1 is located at the mouth of Resurrection Bay near Seward, Alaska and is the station closest to shore on the Seward Line transect. Temperature and salinity versus depth profiles have been taken at this oceanographic station since December 1970. The data is only available in 10 to 25 m increments to a depth of 100 m, although the increments greater than 10 m were deeper than 30 m. The data collected by the PMEL group in 2001 is only available in 10 m increments to a depth of 100 m.

Stations where hydrographic samples were collected were grouped over regional spatial scales of about 500 km (Mueter *et al.,* 2005) (Figs 3.3 and 3.4), corresponding to the dominant scale of covariation among the survival rates of pink salmon stocks (Pyper *et al.*, 2001). Three regions are in the downwelling domain of the northeast Pacific (Kodiak, central GOA, Yakutat) and one region is in the upwelling domain of the northeast Pacific (WCVI).

Within the three regions within the downwelling domain, a further division was made using oceanographic data to categorize each transect's stations based on surface salinity: *inner shelf* water mass = salinity < 30 at 2 m depth or *outer shelf* water mass = salinity $\geq$ 31.5 at 2 m depth. These categories were assigned because salinity gradients can affect the distribution of forage fishes (Abookire and Piatt, 2005), pre-migration sea surface salinity can affect the survival of pink salmon fry (Mueter *et al.,* 2005), and different processes influence stratification on the inner and outer GOA shelf (Weingartner, 2007).

Due to limited stability data in the *inner shelf* water mass, only the central GOA region represented the downwelling domain. For the *outer shelf* water mass data, the central GOA, Kodiak, and Yakutat regions represented the downwelling domain (Table 3.2).

Instead of using surface salinity to divide the water mass, the stations within the WCVI region were divided into inner shelf stations (WCVI *inner shelf*), and shelf break/slope stations (WCVI *outer shelf*) at the 200 meter depth contour (Fig. 3.4). The

currents along the inner shelf differ from those along the shelf break (Freeland *et al.,* 1984; Thomson *et al.,* 1989).

Stability has a strong seasonal pattern; it begins to increase in the spring and levels off in the summer (Dobbins *et al.,* 2009). To remove the seasonal pattern, six locally weighted regression scatterplot smoothing (LOWESS) models using a range of smoothness parameters ($f = 0.2 - 0.9$) were fit to the hydrographic samples, grouped as follows: 1. the *inner shelf* water mass of the central GOA region, 2. the *outer shelf* water mass of the central GOA region, 3. the *outer shelf* water mass of the Kodiak region, 4. the *outer shelf* water mass of the Yakutat region, 5. the *inner shelf* of the WCVI region, and 6. the *outer shelf* of the WCVI region (Fig. 3.5). Smoothing parameters of 0.70, 0.85, 0.80, 0.70, 0.85, and 0.80, respectively, were used. Residuals from the LOWESS fits were then calculated for each hydrographic sample. Within each region and water mass, an average stability residual by year was calculated (Fig. 3.6). If the residual was positive (negative), the average stability was greater (less) than the average stability across all years, by region and water mass.

Data Analysis

The analysis of potential relationships between stability during the release year and hatchery pink salmon survival rates the following year proceeded in the following steps: determine which stability region to correlate with the survival rates from each hatchery of origin, compute single-stock models, create multi-stock models, and lastly determine the best model using the Akaike Information Criterion, corrected for small sample sizes (AICc) (Burnham and Anderson, 1998) and likelihood ratio tests (LRTs).

In the first step, the stability region most appropriate to correlate with the individual hatchery of origin survival rates was determined based on prior studies (Table 3.1). Ocean sampling studies (Farley and Munk, 1997; Pyper *et al.,* 2001) have determined the principal areas of residence for juvenile pink salmon from many pink salmon stocks. Since the dominant scale of covariation among the survival rates of pink

salmon stocks is roughly 500 km (Pyper *et al.,* 2001), and the direction of ocean migration of pink salmon after they leave the hatchery is known, hatcheries within similar regions were grouped together and individual stock survival rates from the following year were correlated with one of four stability regions in the direction of ocean migration (Table 3.1).

Single Stock Models

The standard model used in population ecology assumes that there is no relationship among populations (stocks) of the same taxonomic group (Myers *et al.,* 2001). In the second step, a preliminary analysis using single stock models was done to examine the magnitude of the distribution of parameters (α, β, δ) from the single stock models, and to identify geographic or bathymetric patterns in the environmental covariates. Stability effects were estimated for each stock *i* separately in the generalized Ricker model (Quinn and Deriso, 1999),

$$y_{i,t+1}=\alpha_i - \beta_i R_{it} + \delta^j X_{it} + \varepsilon_{it}; \quad \varepsilon_{it} \sim N\left(0, \sigma_y^2\right). \tag{3.2}$$

In this single stock model, y is the transformed survival for the i-th stock in year t+1, R_{it} is the hatchery fry releases (x 10^{-7}) for the i-th stock in year t, α_i is the stock-specific productivity parameter, β_i is the stock-specific magnitude of density dependence, and ε_i is a random error term, $\varepsilon_i \sim N(0, \sigma_y^2)$. The environmental effects (δ) were modeled with X, a stock-specific (Table 3.2) measure of coastal stability during the year of release, for either the inner or outer shelf (j); stocks within the same region were compared to the same stability measurements. If a stock did not have at least three years of survival data with corresponding stability effects calculated for each year, the stock was not used in the single-stock analysis.

Multi-Stock Models

In step three, several multi-stock mixed effects models were created. Linear mixed-effects models, a type of hierarchical model, are suitable in cases where multiparameter models (i.e., spawner-recuit) are fitted to a wide range stocks which are expected to have similar responses (Mantzouni *et al.,* 2010). In this study, models combined parameters that were associated with the entire northeast Pacific pink salmon population (fixed effects) and parameters that were associated with individual pink salmon stocks (random effects). The β parameter depends on habitat size and suitable habitat which varies across regions and can be influenced by ecosystem variables (Kell *et al.,* 2005); therefore, a β parameter was estimated for each stock separately in all models. A fixed intercept common to all stocks (α) with random stock-specific effects (a_i) (model form 'a') or a domain-specific intercept (α_k) with random stock-specific effects (model form 'b') were estimated for all models.

Several model forms for stability effects were investigated for both the inner and outer shelf data (Table 3.3 and Table 3.4): no stability effects (model 1), stability effects that varied by region (central GOA *inner shelf*, WCVI *inner shelf*) (model 2), stability effects that varied by region with random stock specific stability effects (model 3), stability effects that varied by domain (one or more regions combined; upwelling or downwelling) (model 4), stability effects that varied by domain with random stock specific stability effects (model 5), a mean stability effect (across all regions and domains) (model 6), and a mean stability effect with random stock specific stability effects (model 7). Models 2 and 4 were the same for the inner shelf water mass only. For the outer shelf data, stability effects that varied by region included central GOA *outer shelf*, Kodiak *outer shelf*, Yakutat *outer shelf*, and WCVI *outer shelf*. The most complex model contained domain-specific intercepts along with random stock-specific deviations of productivity, stability effects that varied by region with random stock specific stability effects, and stock-specific density dependence,

$$y_{i,t+1}=\alpha_k + a_i - \beta_i R_{it} + \delta_r^j X_{it} + g_i^j X_{it} + \varepsilon_{it};\ \varepsilon_{it}\sim N\left(0,\sigma_y^2\right). \quad (3.3)$$

In equation 3.3, y is the transformed survival for the ith stock in year t+1, R_{it} is the hatchery fry releases (x 10^{-7}) for the i-th stock in year t, α_k is a domain-specific intercept with random stock-specific deviations of productivity (a_i), β_i is the stock-specific magnitude of density dependence, and ε_i is a random error term, $\varepsilon_i \sim N(0,\sigma_y^2)$. The effects of stability (δ) during the year of fry release includes a common regional effect (r) along with random stock specific effects (g_i^j), using either the inner or outer shelf (j) stability data. In equation 3.3, stocks within the same region had the same stability measurements. Both random stock-specific deviations in productivity and random stock-specific effects of stability were assumed to follow a joint normal distribution with means 0, variances σ_a^2 and σ_g^2, and covariance σ_{ag}.

Using the maximum likelihood fits, models were compared using AICc. To determine the range of plausible models, the AICc score for each model was rescaled relative to the model with the lowest AICc value. Models with $\Delta \leq 2$ were considered equally plausible, while a model with $\Delta > 10$ was considered not competitive (Burnham and Anderson, 1998). Sensitivity analyses were then performed on competitive models only.

Sensitivity Analysis

Mixed effects models assume that; (1) the within-group errors are independent and identically normally distributed with mean 0 and variance σ^2 and that they are independent of the random effects, and (2) the random effects are normally distributed with mean 0 and covariance matrix Ψ (not depending on the group) and are independent for different groups (Pinheiro and Bates, 2000). For the best model(s), chosen by AICc, using the inner and outer shelf data, these two assumptions were tested.

To test assumption one, diagnostic plots such as within-group residuals, standardized residuals versus within-group fitted values, and normal probability plots of the residuals were investigated. LRTs were performed between models with (subscript 1) and without autocorrelation and between models with (subscript 2) and without heteroskedasticity of the within-group error. Survival estimates are often autocorrelated over time and preliminary analysis of single stock residuals revealed possible patterns in the residuals. Stock-specific first-order autoregressive coefficients ϕ_i were estimated for the best model fits by,

$$\varepsilon_{it} = \phi_i \varepsilon_{i,t-1} + \upsilon_t, \tag{3.4}$$

where $\upsilon_t \sim N(0, \sigma^2)$. To test assumption two, diagnostics plots such as the normal probability plot of estimated random effects were investigated. If assumptions were not met, models were restructured.

After sensitivity analyses were preformed, final mixed effects model parameters were estimated using restricted maximum likelihoods (REML). Although the REML fits are less biased, model fits cannot be compared (Pinheiro and Bates, 2000).

RESULTS

Single Stock Models

Although there was not a clear pattern in stability effects as latitude increased, there was a distinction between stability effects and marine survival in the inner versus outer shelf (Fig. 3.7). Within the inner shelf, the stability coefficients ranged from -0.0025 to 0.0005 and only two of the coefficients from the downwelling domain were slightly above zero (AFKa, SGHa), while in the outer shelf the stability coefficients had a larger range from -0.0137 to 0.0016 and were evenly distributed above and below zero (open circles; Fig. 3.8).

Multi-Stock Models

For models fit to the inner shelf stability data, marine survival rates increased for salmon that experienced below-average stability on the inner shelf during early marine residence (Fig. 3.8; left panel). Based on the ΔAICc scores, there were two competing models (models 4a and 4b; Table 3.3). The two best model fits were models with a common or domain-specific intercept with random stock-specific deviations of productivity, and stability effects that varied by domain. The inclusion of stock-specific first-order autoregressive coefficients (model $4a_1$, model $4b_1$) and the assumptions of mixed effects models (model $4a_2$, model $4b_2$) were then tested for in models 4a and 4b using LRTs (Tables 3.5 and 3.6). Neither autocorrelation nor heteroskedasticity of within-group variances were important in either model (Table 3.6). After these sensitivity analyses, the final best model fits were models 4a and 4b. The parameters of these final mixed effects model parameters were then estimated using REML (Table 3.7).

In these final best models using stability data from the inner shelf, stability coefficients were negative for the downwelling and upwelling domains. While both stability coefficients were significant in model 4b, only the upwelling domain stability coefficient was significant in model 4a (Table 3.7); the confidence interval of the stability coefficient for the downwelling domain included zero in model 4a. Therefore, the best model using stability data from the inner shelf was model 4b.

Excluding the PIH stock from the central GOA region, the estimated beta parameter ranged from -0.1387 to 0.8169 in the upwelling domain and from -0.0994 to 0.0029 in the downwelling domain in model 4b (Fig. 3.9; left panel). The PIH stock had a particularly small estimated beta parameter, -14.7205. This stock was not included in Fig. 3.9. Only the QRHc and the MBH stocks had significant beta parameters at the $P \leq 0.05$ level.

For models fit to the outer shelf stability data, stability effects from the outer shelf showed no consistent relationship to marine survival within the northeast Pacific Ocean (Fig. 3.8; right panel). Based on the ΔAICc scores, there was only one competing

model (model 1b; Table 3.4). This model contained domain-specific intercepts with random stock-specific deviations of productivity and no stability effects. The inclusion of stock-specific first-order autoregressive coefficients (model $1b_1$) and the assumptions of mixed effects models (model $1b_2$) were then tested for in model 1b using LRTs (Tables 3.5 and 3.6). Neither autocorrelation nor heteroskedasticity of within-group variances were important in this model. After these sensitivity analyses, the final best model fit was model 1b. The parameters of these final mixed effects model parameters were then estimated using REML (Table 3.7).

In the final best model using stability data from the outer shelf, stability coefficients were not included in model 1b. Therefore, stability effects from the outer shelf showed no consistent relationship to marine survival within the northeast Pacific. Excluding the PIH stock from the central GOA region and the BRC stock from the Yakutat region, in model 1b the estimated beta parameter ranged from -0.0765 to 1.1483 in the upwelling domain and from -0.2328 to 0.0098 in the downwelling domain (Fig. 3.9; right panel). The PIH stock had a particularly large estimated beta parameter, 272.0772, and the BRC stock had a particularly small estimated beta parameter, -4.6664. These stocks are not included in Fig. 3.9. Only the KBH, PRCc, QRHc, and the TBH stocks had significant beta parameters at the $P \leq 0.05$ level.

DISCUSSION

Salmon abundance and survival rates in the upwelling and downwelling domains of the northeast Pacific Ocean are often asynchronous (Francis and Sibley, 1991). This inverse relationship is linked to large-scale climatic patterns such as the Pacific Decadal Oscillation (Mantua *et al.,* 1997; Hare *et al.,* 1999) and the strength of the Aleutian Low Pressure System (Beamish and Bouillon, 1993). More recent work suggests that survival rates covary at regional scales and that local environmental conditions have a greater influence on survival rate and recruitment patterns than these larger, ocean-basin scale oceanographic patterns (Pyper *et al.,* 2001; Mueter *et al.*, 2002b). During early marine

residence, warm anomalies in coastal sea surface temperatures (SSTs) are associated with an increase in survival rate for Alaskan sockeye (*O. nerka*), chum (*O. keta*), and pink salmon stocks and a decrease in survival rate for sockeye and pink salmon stocks from British Columbia and Washington (Mueter *et al.,* 2002a). Survival rates of hatchery stocks of coho salmon (*O. kisutch*) form northern and southern clusters that divide at the northern end of Vancouver Island (Hobday and Boehlert, 2001). Within the same species, sockeye, chum, and pink salmon survival rates positively covary at regional scales among Pacific Northwest and Alaskan stocks, but do not covary at broader-scales (Peterman *et al.,* 1998; Pyper *et al.,* 2001; Pyper *et al.,* 2002).

Prior studies that have focused on localized environmental variables that affect salmon survival have supported the hypothesis that within the coastal downwelling domain of the northeast Pacific Ocean, salmon survival should improve when water column stability within coastal regions increases, while water column stability should have the opposite effect on marine survival within the upwelling domain (Gargett, 1997). Cooler SSTs during the winter prior to smolt migration, which are associated with weaker spring stratification, lead to higher smolt to adult survival of Oregon Production Index coho salmon in the upwelling domain (Logerwell *et al.,* 2003). In the coastal Gulf, increased water column stability was linked to increased chlorophyll-*a* concentrations, longer bloom duration, and earlier onset of the spring bloom supporting a link between primary production and water column stability (Henson, 2007).

Based on the recent findings that regional-scale processes dominate interannual variations in survival rates of salmon, and support for the optimal 'window' stability hypothesis in both downwelling and upwelling domains, the relationships between regional water column stabilities during early marine residence and marine survival rates of hatchery pink salmon stocks the following year were explored. Contrary to expectation, findings were similar between the upwelling and downwelling domains, but differed by the distance offshore. Marine survival rates of hatchery pink salmon from northern and southern stocks increased for salmon that experienced below-average

stability on the inner shelf during early marine residence while stability effects from the outer shelf showed no consistent relationship to marine survival within the northeast Pacific Ocean. Juvenile salmon distribute themselves across the entire continental shelf in surface waters but are rarely found beyond the continental shelf (Welch *et al.,* 2003), supporting the contention that the outer shelf would play less of a role in the variability in salmon survival during the year of release. Other studies have found that similar environmental factors affect salmon survival rates in the upwelling and downwelling domains synchronously. For example, although the time period between the domains differed, a shallow mixed layer depth was associated with increased survival of hatchery coho salmon stocks from northern California to Kodiak Island, Alaska. While the mixed layer depth at the time of return was more important for northern stocks, the mixed layer depth at the time of release was more important for southern stocks (Hobday and Boehlert, 2001).

There were a few main limitations in this study. The first limitation of the study was the mismatch between available time series data for both salmon survival and water column stability data. While there is a long time series of stability data for the west coast of Vancouver Island shelf and slope (1980-2008), there are a limited number of stocks and survival data for this region (five stocks, 4 to 14 years of survival data). On the other hand, the Kodiak and Yakutat regions have limited stability data collected within the inner shelf water mass (<20 hydrographic samples per region during the study time period) but extensive survival data (i.e., Kitoi Bay Hatchery (brood years 1976-2007); Sheldon Jackson Hatchery (brood years 1975-2007)). There were so few stability samples within the inner shelf water mass, the Kodiak and Yakutat regions were not included in the inner shelf models. This mismatch limited the number of datapoints available for identifying any relationships between stability during early marine residence and survival the following year. A linear mixed-effects model, a type of hierarchical model, is a rigorous probabilistic framework for combining data and making inferences across independent stocks with analogous characteristics that are assumed to show similar

patterns in their dynamics (Gelman and Hill, 2007). Since information is combined across multiple stocks, strength for the estimation of individual parameters is borrowed from the broader dataset and there is reduced uncertainty in the estimation of model parameters for shorter time-series (Myers, 2001; Ntzoufras, 2009).

The second main limitation of this study was that the waters off the west coast of Vancouver Island experience seasonal upwelling in the summer rather than year-round upwelling such as the waters off southern Oregon and northern California. The coastal ocean off the west coast of Vancouver Island has been shown to function as a northern regime; chum salmon throughout the coastal waters of southern British Columbia had lower survival rates when regional stability was lower (Gargett *et al.*, 2001). While the spawning grounds of pink salmon in North America range from central California to near the MacKenzie River in arctic Canada, substantial spawning runs only range from Puget Sound Washington northward, and the greatest population abundances along the North American coast are from central and southeastern Alaska (Vernon *et al.*, 1964; Heard, 2003). Distinct northern and southern groups of wild pink salmon stocks divide above the Queen Charlotte Islands (Mueter *et al.,* 2002a). Therefore, it would not make sense biologically to sample stability from a year-round upwelling domain such as southern Oregon and northern California. Stratification within a 'true' year-round upwelling region could be matched with juvenile marine survival of salmon species whose distribution ranges farther south such as coho and Chinook (*O. tshawytscha*) salmon. These species of salmon may better test the hypothesis of a positive association with stratification within the coastal downwelling domain and a negative association with stratification within the southern downwelling domain.

The final limitation of this study was that the framework of models using the linearized and generalized Ricker spawner recruit function for species of the family Salmonidae has produced both biologically and statistically meaningful results (Myers *et al.,* 1999; Mueter *et al.,* 2002a), but may also lead to estimation difficulties because of the large number of fixed effects (Myers *et al.,* 2001). A separate slope (fixed effect) is

estimated for each stock: 15 and 18 of the estimated parameters in the models in the inner and outer shelf models, respectively.

Prior studies using the linearized Ricker spawner recruit model with pink salmon data from British Columbia, Alaska, Kamchatka, and Sakhalin Island in a mixed-model framework have found that the true range of the intercept across all areas is very small. The order of magnitude difference in estimation of stock productivity in the single stock models is due to estimation error in individual stock analyses (Myers *et al.,* 1999). Therefore, a fixed intercept common to all stocks with random stock-specific effects is recommended as the best parameterization. In the modeling framework of this study, both domain-specific intercepts and a common intercept were allowed. Although the intercept for the downwelling and upwelling domain were similar, the best fit models in both the inner and outer shelf contained domain-specific intercepts. Further understanding of how regional oceanographic processes such as stability affect the survival rate of juvenile salmon in the upwelling and downwelling domains of the northeast Pacific Ocean will lead to better management and better predictions of climate changes effects on Pacific salmon.

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FIGURES

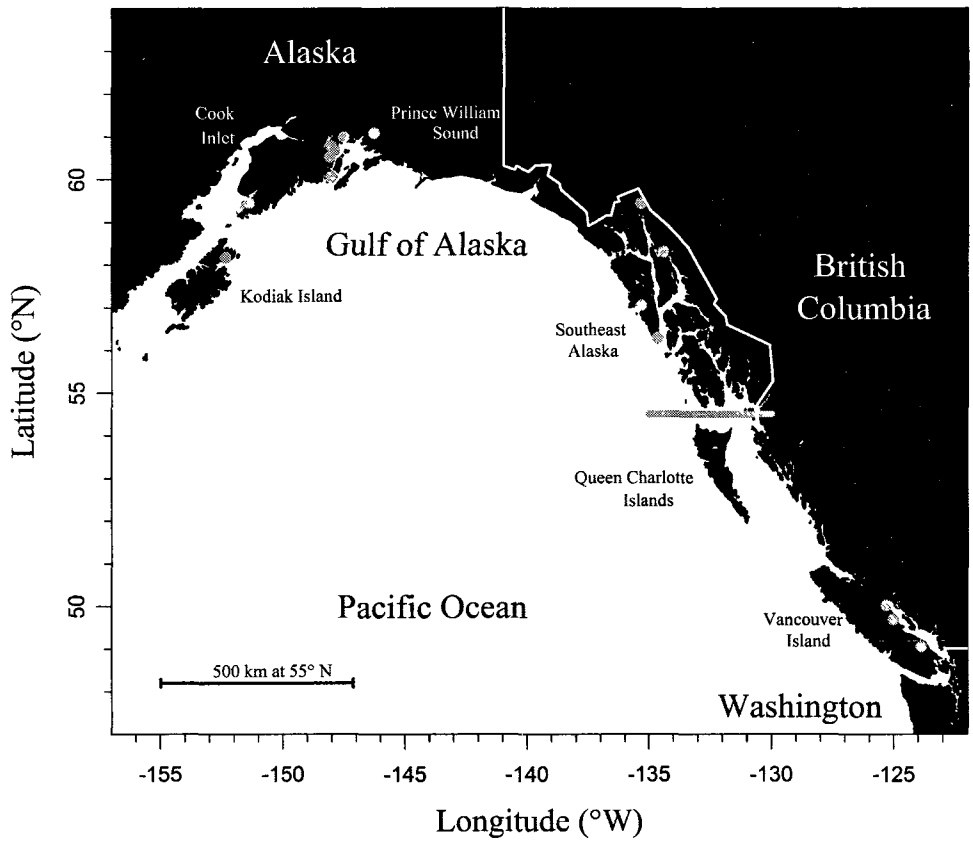

Figure 3.1 Locations of the 16 pink salmon hatcheries (grey circles). The thick, grey horizontal line divides the northern and southern pink salmon stocks.

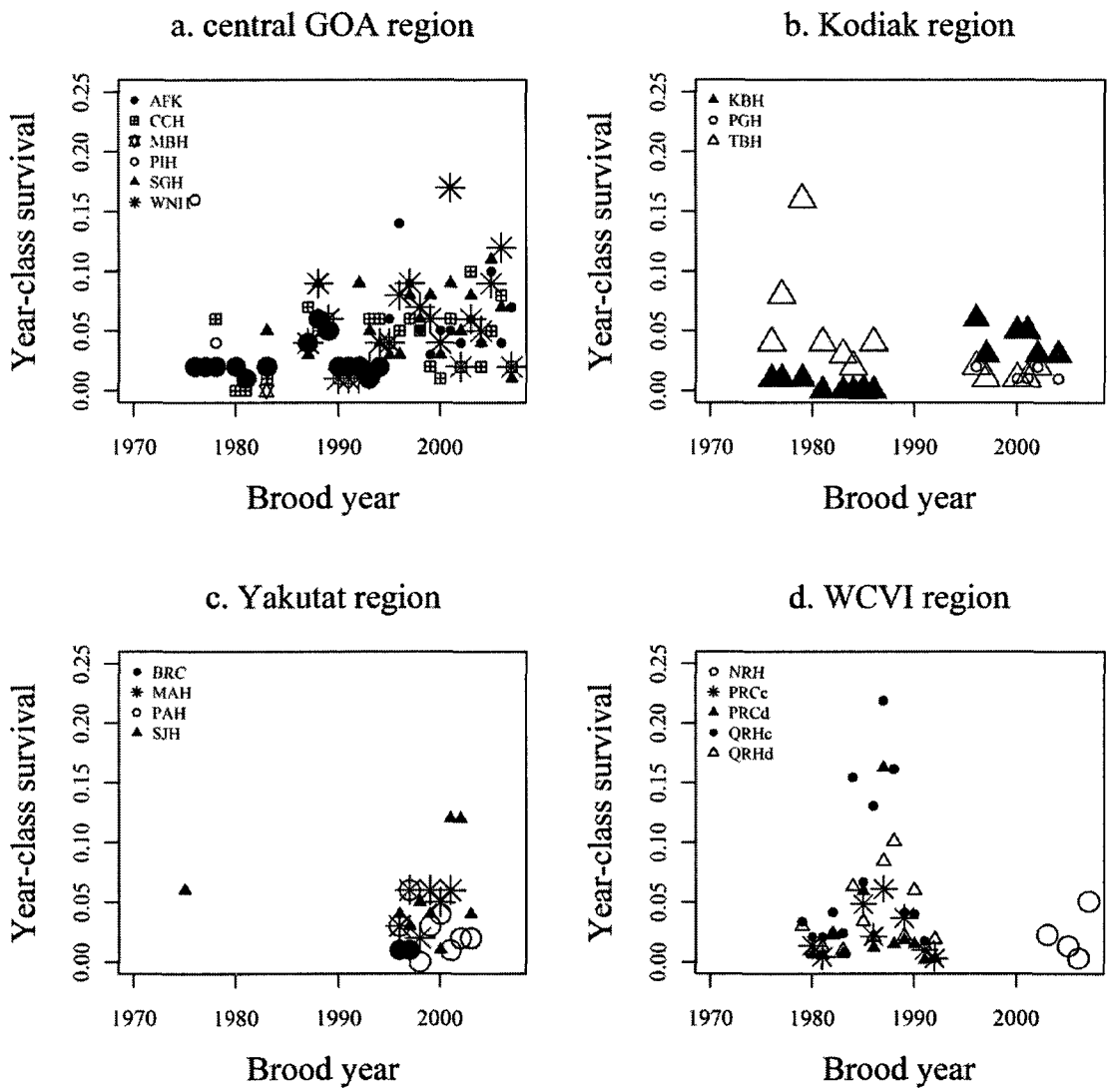

Figure 3.2 Year-class survival by brood year. The figures are separated by regional location.

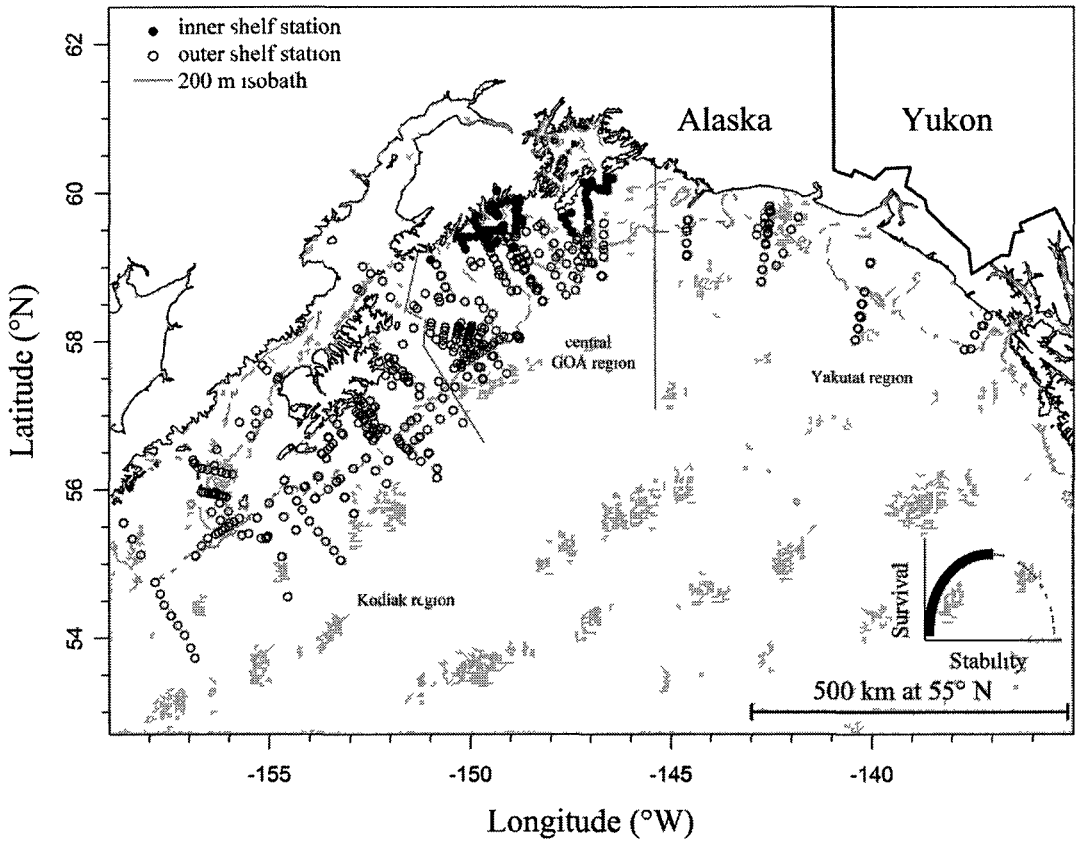

Figure 3.3 Stations where hydrographic information was collected within the downwelling domain of the coastal Gulf of Alaska. Stability residuals were averaged over the three geographic regions. Based on surface salinity, the stations in the three regions were further separated by water mass: inner shelf or the outer shelf. Inner shelf stations were only in the central GOA region for this study. Salmon survival is hypothesized to be favored within the downwelling domain if water column stabilities increase, whereas stability may have the opposite affect at lower latitudes (Gargett, 1997).

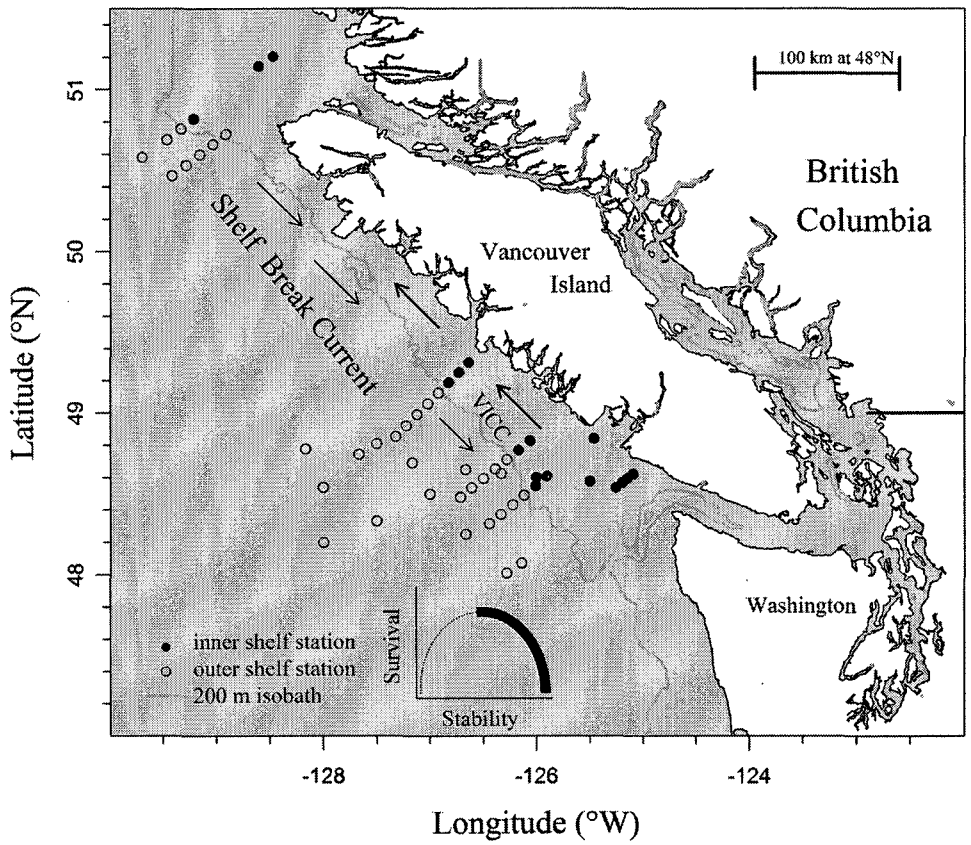

Figure 3.4 Stations where hydrographic information was collected within the upwelling domain off the west coast Vancouver Island (WCVI). Based on the 200 meter depth contour, the stations within the WCVI region were further divided into inner shelf and outer shelf stations. Salmon survival is hypothesized to be favored within the downwelling domain if water column stabilities increase, whereas stability may have the opposite affect at lower latitudes (Gargett, 1997). Vancouver Island Coastal Current (VICC)

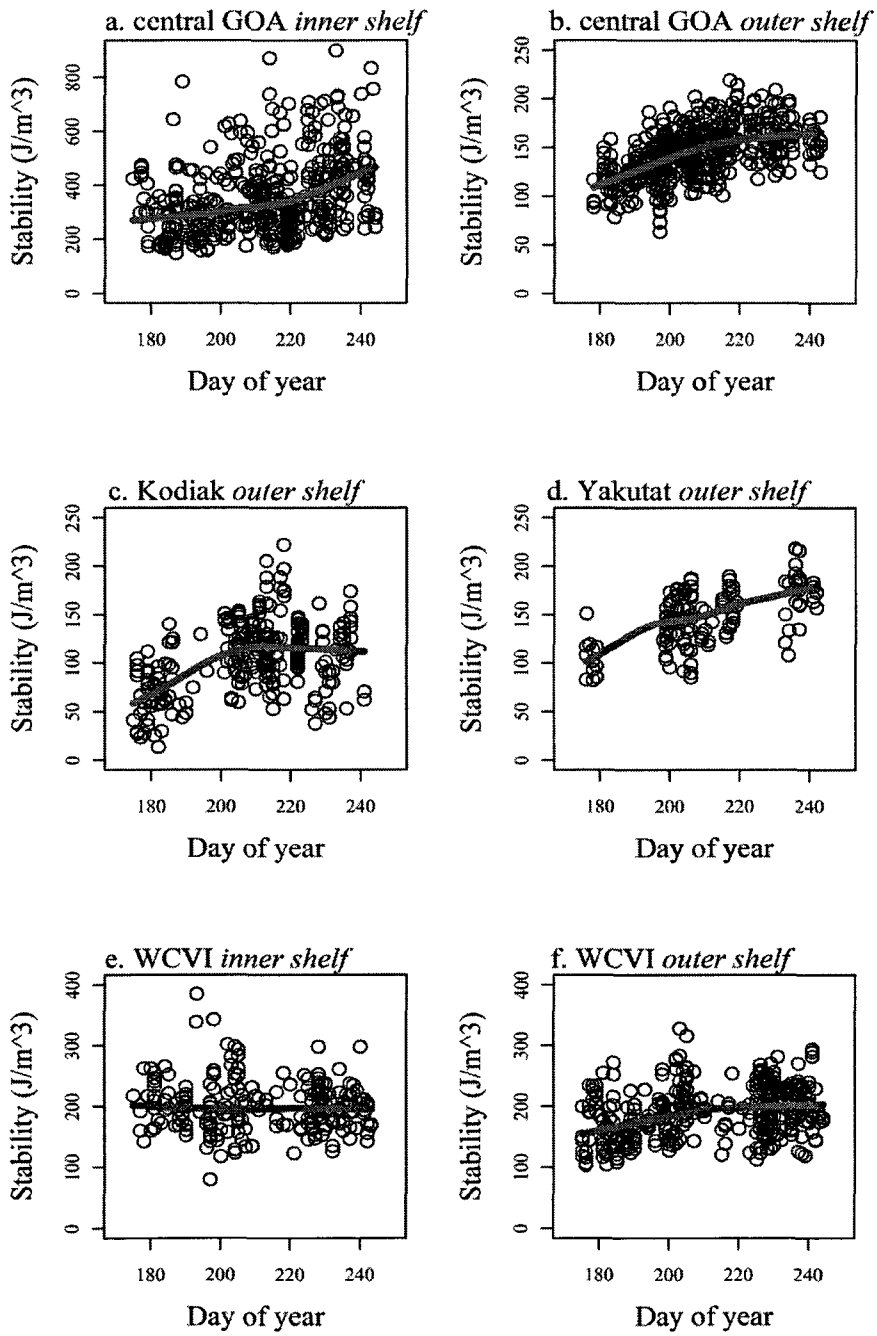

Figure 3.5 LOWESS models fit to the hydrographic samples by day of year, separated by water mass and region.

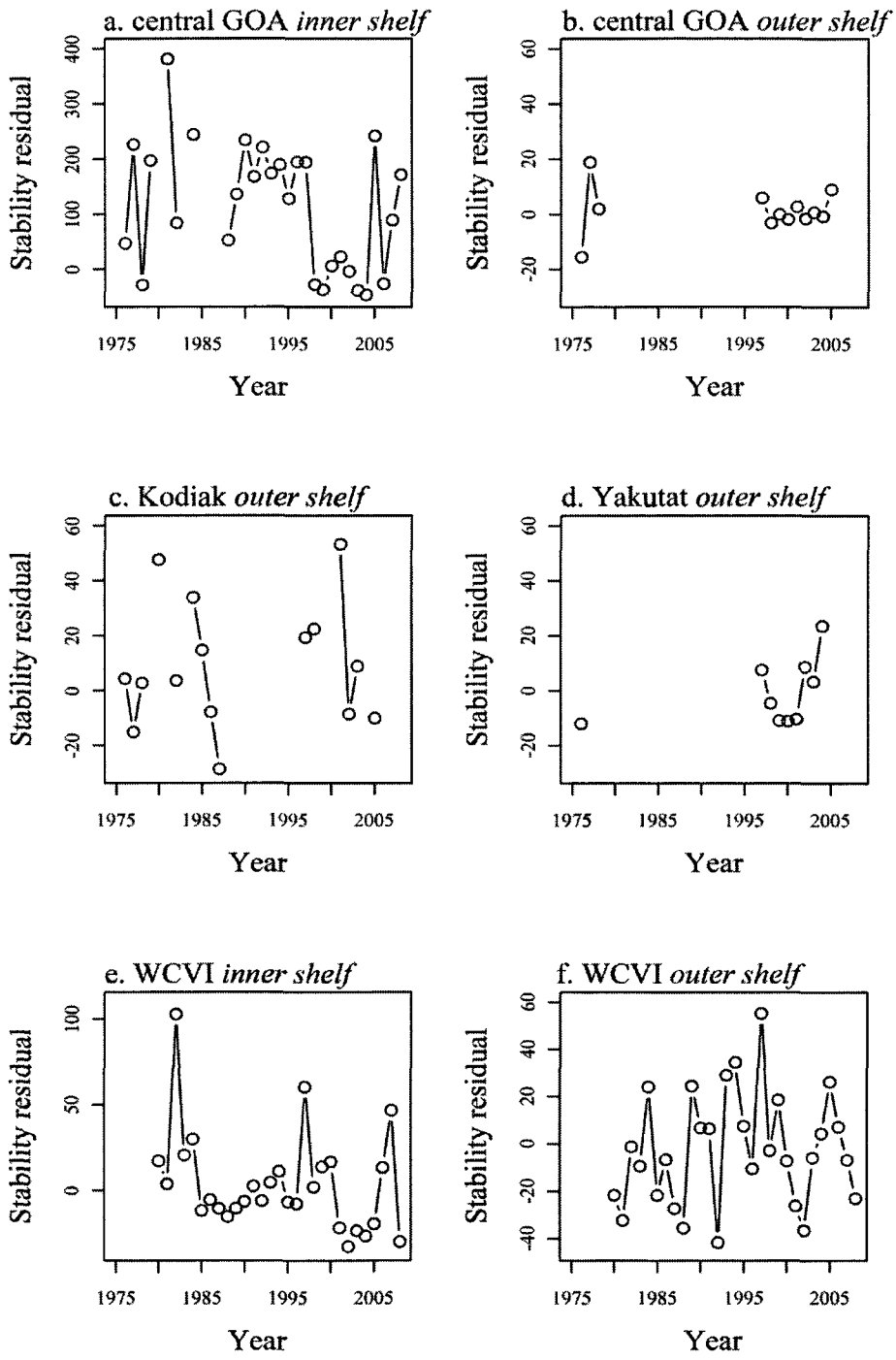

Figure 3.6 Average stability residual by year, separated by water mass and region.

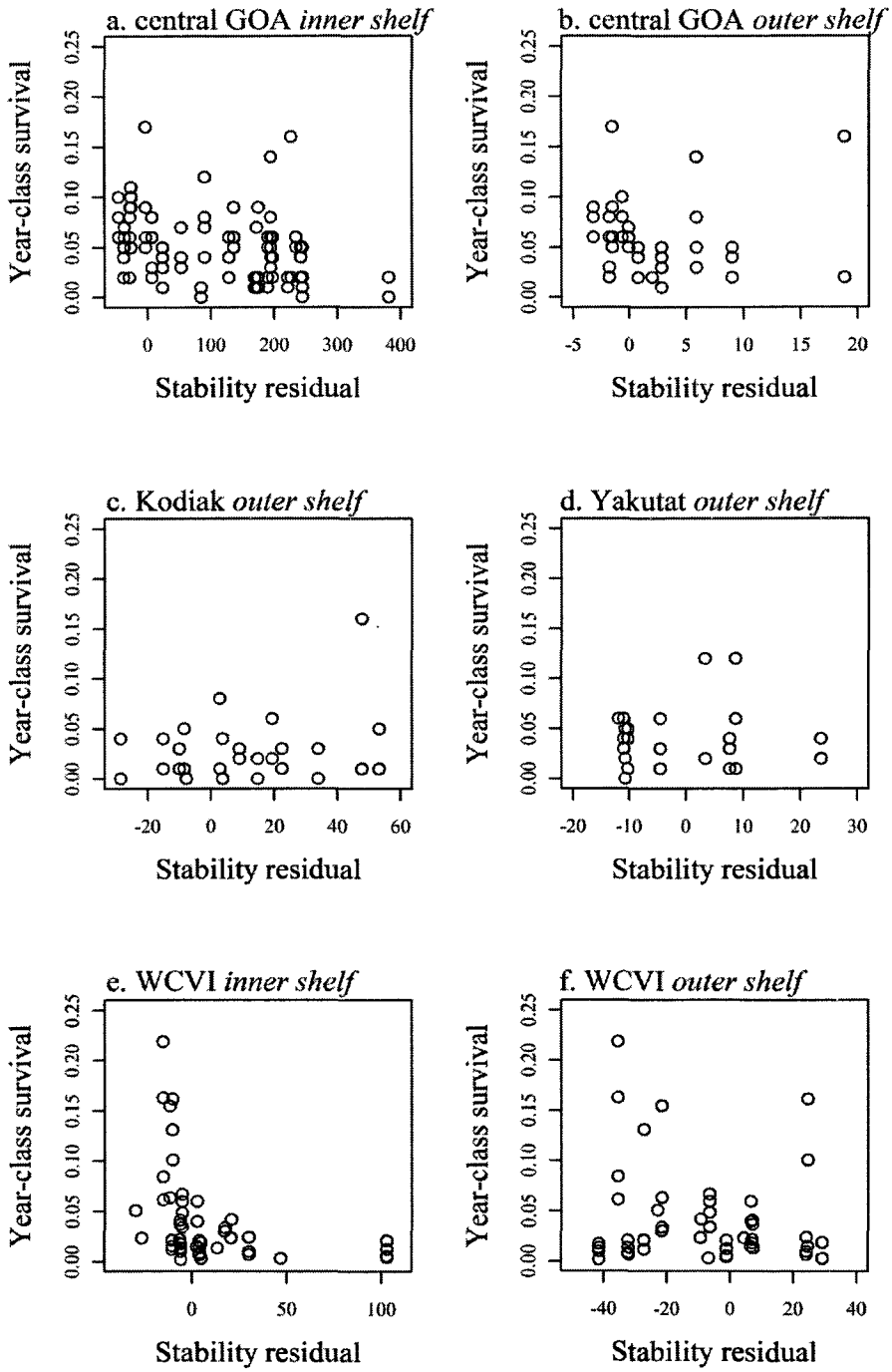

Figure 3.7 Year-class survival by stability residual (during the year of release) separated by water mass and region.

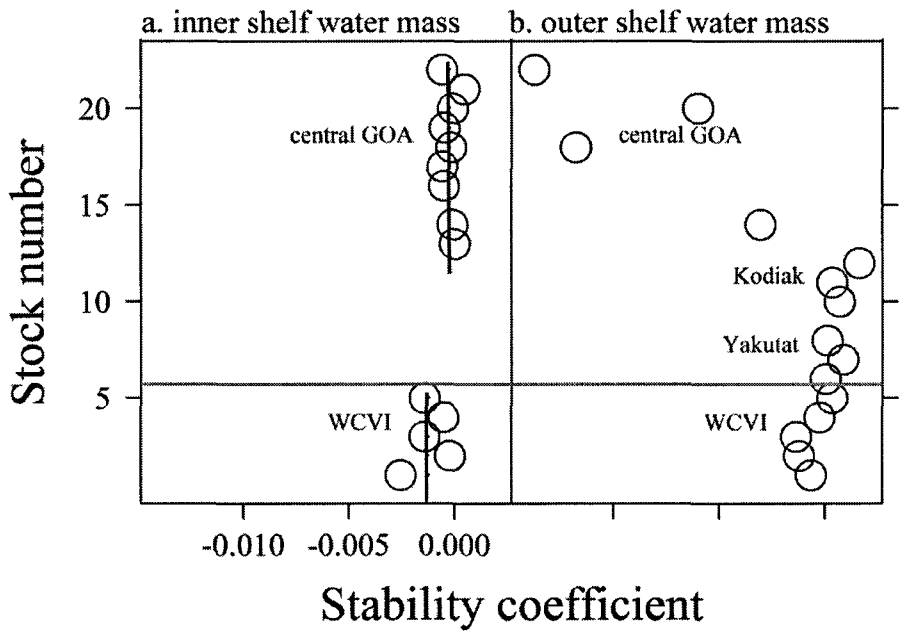

Figure 3.8 Estimated coefficients for the effects of stability (δ) on marine survival by latitude (stock number) for the single stock and multi-stock mixed effects models. Stability coefficients are represented by large open circles for the single-stock models. Stocks with less than three years of survival data with corresponding stability effects calculated for each year were not used in the single-stock analysis. The grey horizontal line divides the downwelling (upper) and upwelling (lower) pink salmon stocks. The solid vertical lines are the stability coefficients from the multi-stock model fit to the inner shelf water mass data, model 4b.

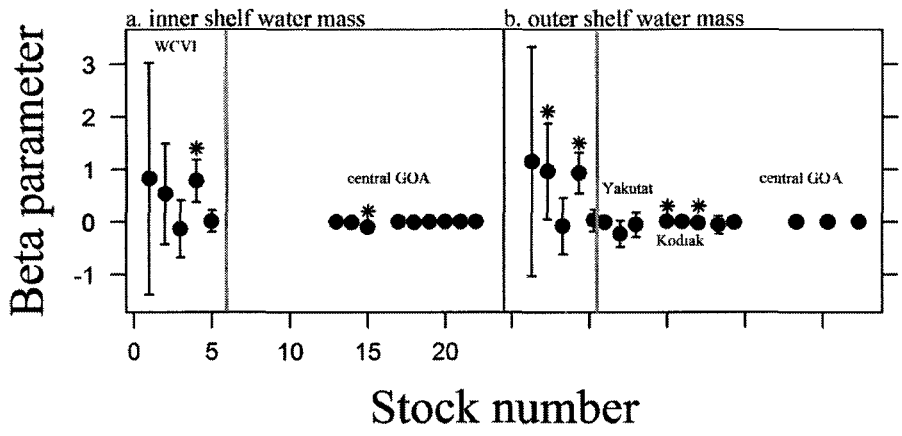

Figure 3.9 Estimated beta parameters, with 95% confidence intervals, for the multi-stock mixed effects models fit to the inner shelf water mass (model 4b) and outer shelf water mass (model 1b) data. The grey vertical lines divide the downwelling (right) and upwelling (left) pink salmon stocks. Two stocks are not shown (PIH, BRC). The parameters that were significant at the $P \leq 0.05$ level are starred.

TABLES

Table 3.1 Summary of the 22 hatchery pink salmon stocks from Kodiak Alaska to Vancouver Island British Columbia; N_I is the number of brood years (brood years$_I$) used in the inner shelf models; N_O is the number of brood years (brood years$_O$) used in the outer shelf models; subscript *a* refers to fish that were coded wire tagged; subscript *b* refers to fish with thermally marked otoliths; subscript *c* refers to fed fry; subscript *d* refers to unfed fry; na: not applicable

Domain	Stability region	Hatchery	Abbreviation	Stock number	Brood years$_I$	N_I	Brood years$_O$	N_O	Source[a]
downwelling	central GOA	Armin F Koernig Hatchery	AFK_a	13	1976-1978, 1980, 1981, 1983, 1987-1994	14	1976-1977	2	1
downwelling	central GOA	Armin F Koernig Hatchery	AFK_b	14	1995-2007	13	1996-2004	9	2
downwelling	central GOA	Cannery Creek	CCH_a	19	1978, 1980, 1981, 1983, 1987-1994	12	na	na	1
downwelling	central GOA	Cannery Creek	CCH_b	20	1995-2007	13	1996-2004	9	2
downwelling	central GOA	Main Bay Hatchery	MBH	15	1983	1	na	na	1
downwelling	central GOA	Perry Island Hatchery	PIH	16	1976, 1978, 1980	3	1976	1	1
downwelling	central GOA	Solomon Gulch Hatchery	SGH_a	21	1981, 1983, 1987-1994	10	na	na	1
downwelling	central GOA	Solomon Gulch Hatchery	SGH_b	22	1995-2007	13	1996-2004	9	2
downwelling	central GOA	Wally Noerenberg Hatchery	WNH_a	17	1987-1994	8	na	na	1
downwelling	central GOA	Wally Noerenberg Hatchery	WNH_b	18	1995-2007	13	1996-2004	9	2
downwelling	Kodiak	Kitoi Bay Hatchery	KBH	10	na	na	1976-1977, 1979, 1981, 1983-1986, 1996-1997, 2000-2002, 2004	14	1
downwelling	Kodiak	Port Graham Hatchery	PGH	11	na	na	1996,2000-2002, 2004	5	1
downwelling	Kodiak	Tutka Bay Hatchery	TBH	12	na	na	1976-1977, 1979, 1981, 1983-1986, 1996-1997, 2000-2002	13	3
downwelling	Yakutat	Burro Creek Hatchery	BRC	9	na	na	1996-1997	2	1
downwelling	Yakutat	Kowee Creek Macaulay, Sheep Creek	MAH	8	na	na	1996-2001	6	4
downwelling	Yakutat	Port Armstrong Hatchery	PAH	6	na	na	1996-2003	8	1
downwelling	Yakutat	Sheldon Jackson Hatchery	SJH	7	na	na	1975, 1996-2003	9	1
upwelling	WCVI	Nanaimo River Hatchery	NRH	1	2003, 2005-2007	4	2003, 2005-2007	4	5
upwelling	WCVI	Puntledge River Hatchery	PRH_a	2	1980-1981, 1985-1987, 1989, 1991-1992	8	1980, 1981, 1985-1987, 1989, 1991, 1992	8	6
upwelling	WCVI	Puntledge River Hatchery	PRH_d	3	1980-1983, 1985-1992	12	1980-1983, 1985-1992	12	6
upwelling	WCVI	Qunsam River Hatchery	QRH_a	4	1979-1991	13	1979-1991	13	6
upwelling	WCVI	Qunsam River Hatchery	QRH_d	5	1979-1992	14	1979-1992	14	6

[a]1. Alaska Department of Fish and Game, personal communication, August 2010; 2. Steve Moffitt, Area Research Biologist, Alaska Department of Fish and Game, Division of Commercial Fisheries, personal communication, August 2010; 3. Gary Fandrei, Executive Director, Cook Inlet Aquaculture Association, personal communication, August 2010; 4. Rick Focht, Director of Operations, Douglas Island Pink and Chum, Inc., personal communication, August 2010; 5. Brian Banks, Co-manager, Nanaimo River Hatchery, personal communication, July 2010; 6. Joan Bateman, Oceans, Habitat and Enhancement Branch, Department of Fisheries and Oceans, Canada, personal communication, August, 2010.

Table 3.2 Regional spatial scales where hydrographic samples were collected. Within the three regional spatial scales in the northern coastal Gulf of Alaska (Kodiak, central GOA, Yakutat), a further division was made based on surface salinity: inner and outer shelf water masses. Based on the 200 meter depth contour, the stations in the waters off the west coast of Vancouver Island were further divided into inner shelf stations and outer shelf stations. The column labeled 'Model' signifies which model the data was used for, either the inner or outer shelf. *N*: number of stability samples for the region and water mass/location.

Model	Domain	Area	Stability region	*N*	Years	Source[a]
inner shelf	downwelling	Alaska	central Gulf of Alaska	443	1976-1979, 1981, 1982, 1984, 1988-2008	1,2,3,4,5,8
inner shelf	upwelling	Canada	west coast of Vancouver Island	216	1980-2008	7
outer shelf	downwelling	Alaska	Kodiak	292	1976-1978, 1980, 1982, 1984-1987, 1997,1998, 2001-2003, 2005	1,8
outer shelf	downwelling	Alaska	central Gulf of Alaska	568	1976-1978, 1997-2005	1,2,3,4,8
outer shelf	downwelling	Alaska	Yakutat	141	1976, 1997-2004	1,6,8
outer shelf	upwelling	Canada	west coast of Vancouver Island	374	1980-2008	7

[a]1. Jamal Moss and Ed Farley, National Marine Fisheries Service, National Oceanic and Atmospheric Administration (NOAA), Ocean Carrying Capacity Program; 2. Russell Hopcroft and Tom Weingartner, University of Alaska Fairbanks (UAF) Institute of Marine Science, Long Term Observation Program (LTOP) (1998-2004); 3. Suzanne Strom, Western Washington University, and Tom Weingartner, UAF Institute of Marine Science, process-oriented projects (PROCESS) conducted by researchers from NOAA and several universities (2001, 2003). The LTOP and PROCESS cruise data can be accessed at: http://globec.whoi.edu/jg/dir/globec/; 4. UAF U.S. Global Ocean Ecosystem Dynamics Northeast Pacific program (GLOBEC); 5. Oceanographic station GAK 1 (59° 50.7' N, 149° 28.0' W) (http://www.ims.uaf.edu/gak1/, accessed: July 1, 2010) (Royer, 1982; Weingartner *et al.*, 2005); 6. Emily Fergusson and Joe Orsi, Southeast Coastal Monitoring (SECM) research project, National Marine Fisheries Service, NOAA; 7. Fisheries and Oceans Canada. Pacific Region. Institute of Ocean Sciences Data Archive. Ocean Sciences Division. [Internet]. Cited 2010-08-06. Available from: http://www-sci.pac.dfo-mpo.gc.ca/osap/data/default_e.htm; 8. NOAA Pacific Marine Environmental Laboratory (PMEL) oceanographic data, Available from: http://www.epic.noaa.gov/epic/ewb/ewb_selprof.htm. [Internet]. Cited 2011-05-02.

Table 3.3 Summary of the model results for the inner shelf. The best fit models (model 4a, model 4b) using AICc comparison are highlighted. p: number of estimated parameters; n: number of observations in the model; RSSD: random stock specific deviations

Model[a]	Stability description	Intercept	Error structure	Within-group error	ΔAICc	Log likelihood	p
1a	None	common	normal	homoskedasticity	9 1	145 1	18
1b	None	domain-specific	normal	homoskedasticity	8 5	146 7	19
3a	stability effects by region w/ RSSD	common	normal	homoskedasticity	6 2	151 9	22
3b	stability effects by region w/ RSSD	domain-specific	normal	homoskedasticity	5 5	153 6	23
4a	**stability effects by domain**	**common**	**normal**	**homoskedasticity**	**0.8**	**151.9**	**20**
4b	**stability effects by domain**	**domain-specific**	**normal**	**homoskedasticity**	**0.0**	**153.6**	**21**
5a	stability effects by domain w/ RSSD	common	normal	homoskedasticity	6 2	151 9	22
5b	stability effects by domain w/ RSSD	domain-specific	normal	homoskedasticity	5 5	153 6	23
6a	mean stability effect	common	normal	homoskedasticity	8 4	146 7	19
6b	mean stability effect	domain-specific	normal	homoskedasticity	3 4	150 6	20
7a	mean stability effect w/ RSSD	common	normal	homoskedasticity	13 8	146 7	21
7b	mean stability effect w/ RSSD	domain-specific	normal	homoskedasticity	8 8	150 6	22

[a] n=151

Table 3.4 Summary of the model results for the outer shelf. The best fit model (model 1b) using AICc comparison is highlighted. Model 3a did not converge. p: number of estimated parameters; n: number of observations in the model; RSSD: random stock specific deviations; na: not applicable

Model[a]	Stability description	Intercept	Error structure	Within-group error	ΔAICc	Log likelihood	p
1a	None	common	normal	homoskedasticity	3 3	141 2	21
1b	**None**	**domain-specific**	**normal**	**homoskedasticity**	**0.0**	**144.2**	**22**
2a	regional stability effects	common	normal	homoskedasticity	12 8	142 1	25
2b	regional stability effects	domain-specific	normal	homoskedasticity	8 0	146 0	26
3a	*stability effects by region w/ RSSD*	*common*	*normal*	*homoskedasticity*	*na*	*na*	*na*
3b	stability effects by region w/ RSSD	domain-specific	normal	homoskedasticity	14 0	146 0	28
4a	stability effects by domain	common	normal	homoskedasticity	7 4	141 9	23
4b	stability effects by domain	domain-specific	normal	homoskedasticity	3 5	145 3	24
5a	stability effects by domain w/ RSSD	common	normal	homoskedasticity	13 2	141 9	25
5b	stability effects by domain w/ RSSD	domain-specific	normal	homoskedasticity	9 3	145 3	26
6a	mean stability effect	common	normal	homoskedasticity	6 0	141 2	22
6b	mean stability effect	domain-specific	normal	homoskedasticity	2 6	144 3	23
7a	mean stability effect w/ RSSD	common	normal	homoscedasticity	11 7	141 2	24
7b	mean stability effect w/ RSSD	domain-specific	normal	homoscedasticity	8 4	144 3	25

[a] n=147

Table 3.5 Summary of the additional models for the inner and outer shelf that were compared to the best fit models (based on AICc comparison) using the likelihood ratio test. p: number of estimated parameters; n: number of observations in the model

Model[a]	Data	Stability description	Intercept	Error structure	Within-group error	Log likelihood	p
$4a_1$	inner shelf	regional stability effects	common	autocorrelated	homoskedasticity	152.0	21
$4a_2$	inner shelf	regional stability effects	common	normal	heteroskedasticity	151.9	21
$4b_1$	inner shelf	regional stability effects	domain-specific	autocorrelated	homoskedasticity	153.9	22
$4b_2$	inner shelf	regional stability effects	domain-specific	normal	heteroskedasticity	153.6	22
$1b_1$	outer shelf	None	domain-specific	autocorrelated	homoskedasticity	144 9	23
$1b_2$	outer shelf	None	domain-specific	normal	heteroskedasticity	144.4	23

[a] n=151 (inner shelf); n=147 (outer shelf)

Table 3.6 Results of the likelihood ratio tests of the best model fits for the inner and outer shelf. LRT: likelihood ratio test

Source	Models contrasted	LRT statistic	*P*
Inner shelf			
Model 4			
Autocorrelation	4a-4a_1	0.1921	0.6611
Heteroskedasticity	4a-4a_2	0.0004	0.9843
Autocorrelation	4b-4b_1	0.4570	0.4990
Heteroskedasticity	4b-4b_2	0.0012	0.9719
Outer shelf			
Model 1			
Autocorrelation	1b-1b_1	1.4634	0.2264
Heteroskedasticity	1b-1b_2	0.3562	0.5506

Table 3.7 Summary of the parameter values, estimated using REML, for the best model fits using the inner and outer shelf stability data. The intercept values show a range since they are the fixed intercept plus the predicted random effect for each stock. SE: standard error; na: not applicable

					Stability effects		
Model	Data	Domain	Region	Intercept	δ	SE (δ)	*P*
4a	inner shelf	downwelling	central GOA	0.3480-0.6288	-0.0002	0.0001	0.0695
	inner shelf	upwelling	WCVI	0.3480-0.6288	-0.0013	0.0004	0.0029
4b	inner shelf	downwelling	central GOA	0.4106-0.6483	-0.0002	0.0001	0.0326
	inner shelf	upwelling	WCVI	0.3280-0.4275	-0.0012	0.0004	0.0058
1b	outer shelf	downwelling	central GOA, Kodiak, Yakutat	0.2690-0.5761	na	na	na
	outer shelf	upwelling	WCVI	0.2676-0.4083	na	na	na

GENERAL CONCLUSION

Regional coastal conditions have a strong influence on juvenile salmon (genus *Oncorhynchus*) survival during their critical first months in the marine environment. Stability-induced changes in the availability of light and nutrients for the production of phytoplankton are reflected in secondary production and could then ultimately affect the marine survival rates of juvenile salmon in the northeast Pacific Ocean. The high latitude downwelling domain (Queen Charlotte Sound to the Aleutian Islands), where macronutrients are plentiful but primary production is limited through low light levels during part of the year, occupies the low-stability end of the optimal 'window.' The low latitude upwelling domain (Baja California to Vancouver Island), where light levels are higher and more uniform throughout the year but macronutrients are limited in the surface layer, occupies the high-stability end of the optimal 'window.' There is a 'window' at intermediate levels of light and nutrients where phytoplankton production is at its maximum. Salmon survival is hypothesized to be favored within the downwelling domain if water column stabilities increase, whereas stability may have the opposite effect at lower latitudes (Gargett, 1997). This study explored the relationship between regional water column stabilities during early marine residence and marine survival rates of pink salmon (*O. gorbuscha*) stocks the following year at both local (Chapter 1 and 2) and broad (Chapter 3) scales within the northeast Pacific Ocean.

In Chapter 2, it was postulated that growth rate and fish condition should increase with decreasing stability within Prince William Sound (PWS) because a slower and weaker development of stratification with a deeper mixed layer depth lengthens phytoplankton production and the interaction between phytoplankton and the springtime zooplankton community, providing more organic matter in the pelagic food webs for salmon (Eslinger *et al.,* 2001). Contrary to expectation, water column stability just prior to capture did not explain the variability in condition index for either hatchery or wild fish collected from within the Sound. As expected, stability within PWS did explain the growth rate of hatchery fish that originated from within the Sound, although stability

explained only a small amount of the variability and did not have the same relationship for each hatchery stock. While the relationship between stability and growth rate was negative for fish from the Armin F. Koernig hatchery (AFK), the Solomon Gulch hatchery (SGH), and the Wally Noerenberg hatchery (WNH) as hypothesized, the relationship was positive for fish from the Cannery Creek hatchery (CCH). On average, CCH releases fry on a later date than the other three PWS hatcheries, and thus juvenile foraging may not be matched to abundant food resources. The juveniles from CCH are released into the Sound as their primary food resource, *Neocalanus*, are declining in abundance.

In Chapter 2, it was also postulated that fish condition should increase with increasing stability within the two water masses, Alaska Coastal Current (ACC) and shelf, of the Gulf of Alaska (GOA). With sufficient light levels, greater water column stability, and shallowing of the mixed layer depth, an increase in primary production during the spring bloom should lead to elevated secondary production and higher marine survival rates of salmon in the Gulf (Miller, 2004). Contrary to expectation, stability effects just prior to capture were not statistically significant in explaining variability in condition index within either Gulf water mass.

For the third hypothesis in Chapter 2, it was postulated that there is an interactive effect between fish condition and water column stability on the variability in year-class survival. Cohorts with individuals heavier at a given length sampled during the year of release within the ACC water mass of the GOA experienced higher survival during the return year, the following spring, but there was no clear relationship between fish condition and survival within the shelf water mass. Fish that migrate to the marine environment at a larger body size tend to have a higher survival rate as compared to their smaller counterparts (Quinn, 2005), but an individual's condition in one life stage may not directly relate to a survival advantage until a later life stage (Zabel and Achord, 2004). The relationship between condition index and year-class survival was positive when stability was below average just prior to capture within PWS; the relationship was

negative when stability was above average. This accords with earlier studies that concluded that slower and weaker development of stratification with a deeper mixed layer depth may be more important for juvenile pink salmon survival in PWS (Eslinger *et al.,* 2001).

Salmon abundance and survival rates in the upwelling and downwelling domains of the northeast Pacific Ocean are often asynchronous (Francis and Sibley, 1991; Hare *et al.,* 1999; Hobday and Boehlert, 2001; Mueter *et al.,* 2002) and the upwelling and downwelling domains occupy opposite ends of the optimal stability 'window' (Gargett, 1997). Therefore, in Chapter 3, it was postulated that in the coastal downwelling domain (southeast Alaska to Kodiak Island) hatchery pink salmon survival should improve when water column stability within coastal regions increases during the summer of early marine residence. Water column stability should have the opposite effect on marine survival within the upwelling domain (west coast of Vancouver Island). Contrary to expectation, based on the results of multi-stock linear mixed-effects models, findings were similar between the upwelling and downwelling domains, but differed by the distance offshore. Marine survival rates of hatchery pink salmon from both northern and southern stocks increased with below-average stability on the inner shelf during early marine residence, while stability effects from the outer shelf showed no consistent relationship to marine survival within the northeast Pacific Ocean.

In conclusion, at a local scale (Chapters 1 and 2) only one strong relationship between water column stability, condition, and marine survival of salmon was found; the relationship between condition index and year-class survival was positive when stability was below average just prior to capture within PWS, and the relationship was negative when stability was above average. At a broad scale (Chapter 3), contrary to expectation, findings were similar between the upwelling and downwelling domains, but differed by the distance offshore.

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